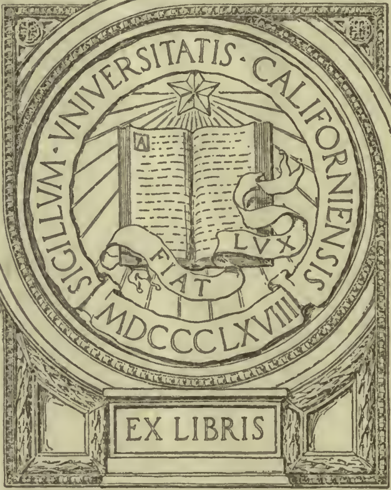
SHOUT
SHARE
IT

MEDICAL SCHOOL
LIBRARY



SIGILLVM · VNIVERSITATIS · CALIFORNIENSIS
FIAT LVX
MDCCCLXVIII
EX LIBRIS

Florence J. Chubb
Memorial.

Florence Chubb.

Digitized by the Internet Archive
in 2007 with funding from
Microsoft Corporation

http://www.archive.org/details/manualzoology00hertrich

A

MANUAL OF ZOOLOGY

BY

RICHARD HERTWIG
Professor of Zoology in the University at Munich

SECOND AMERICAN EDITION FROM THE FIFTH GERMAN EDITION

TRANSLATED AND EDITED BY

J. S. KINGSLEY
Professor of Zoology in Tufts College

NEW YORK
HENRY HOLT AND COMPANY
1905

K H

Copyright, 1902,
BY
HENRY HOLT & CO.

ROBERT DRUMMOND, PRINTER, NEW YORK.

QL 47
H 44 k
1905

PREFACE.

On account of its clearness and breadth of view, its comparatively simple character and moderate size, Professor Richard Hertwig's 'Lehrbuch der Zoologie' has for ten years held the foremost place in German schools. The first or general part of the work was translated in 1896 by Dr. George W. Field, and the cordial reception which this has had in America has led to the present reproduction of the whole.

This American edition is not an exact translation. With the consent of the author the whole text has been edited and modified in places to accord with American usage. For these changes the translator alone can be held responsible. Some of the alterations are slight, but others are very considerable. Thus the group of Vermes of the original has been broken up and its members distributed among several phyla; the account of the Arthropoda has been largely rewritten and the classification materially altered; while the Tunicata and the Enteropneusti have been removed from their position as appendices to the Vermes and united with the Vertebrata to form the phylum Chordata. Other changes, like those in the classification of the Reptilia and the nephridial system of the vertebrates, are of less importance.

A large number of illustrations have been added, either to make clearer points of structure or to aid in the identification of American forms. Except in the Protozoa, American genera have in most cases been indicated by an asterisk. Numerous genera have been mentioned so that the student may see the relationships of forms described in morphological literature.

In the translation the word Anlage, meaning the embryonic material from which an organ or a part is developed, has been transferred directly. As our language is Germanic in its genius, there can be no valid objection to the adoption of the word.

As this work is intended for beginners, no bibliography has been given. A list of literature to be of much value would have been so large as to materially increase the size of the volume. Experience has shown that beginners rarely go to the original sources. This omission is the less important since in all schools where the book is likely to be used other works containing good bibliographies are accessible. Reference might here be made to those in the Anatomies of Lang and Wiedersheim, the Embryologies of Balfour, Korschelt and Heider, Minot, and Hertwig, and Wilson's work on The Cell.

The editor must here return his thanks to Dr. George W. Field for his kindness in allowing the use of his translation of the first part of the book as the basis of the present edition.

J. S. KINGSLEY.

TUFTS COLLEGE, MASS., Sept. 19, 1902.

TABLE OF CONTENTS.

PAGE

INTRODUCTION........ 1

HISTORY OF ZOOLOGY........ 7

DEVELOPMENT OF SYSTEMATIC ZOOLOGY........ 8

DEVELOPMENT OF MORPHOLOGY........ 12

REFORM OF THE SYSTEM........ 18

HISTORY OF THE THEORY OF EVOLUTION........ 19

DARWIN'S THEORY OF THE ORIGIN OF SPECIES........ 25

GENERAL MORPHOLOGY AND PHYSIOLOGY........ 57

GENERAL ANATOMY........ 58

The Morphological Units of the Animal Body........ 58

The Tissues of the Animal Body........ 71

Epithelial Tissues........ 73

Connective Tissues........ 83

Muscular Tissues........ 90

Nervous Tissues........ 94

Summary........ 97

The Combination of Tissues into Organs........ 99

Vegetative Organs........ 102

Organs of Assimilation........ 102

Digestive Tract........ 103

Respiratory Organs........ 107

Circulatory Apparatus........ 109

Excretory Organs........ 115

Sexual Organs........ 117

Animal Organs........ 121

Organs of Locomotion........ 121

Nervous System........ 122

Sense Organs........ 125

Summary........ 131

Promorphology........ 133

GENERAL EMBRYOLOGY........ 139

Spontaneous Generation........ 139

Generation by Parents........ 140

Asexual Reproduction........ 140

Sexual Reproduction........ 142

Combined Methods of Reproduction........ 143

General Phenomena of Sexual Reproduction........ 145

Maturation of the Egg........ 146

Fertilization........ 148

PAGE
Cleavage Processes 151
Formation of the Germ Layers 156
Different Forms of Sexual Development 160
Summary 162
RELATION OF ANIMALS TO ONE ANOTHER 164
Relations between Individuals of the Same Species 164
Relations between Individuals of Different Species 167
ANIMAL AND PLANT 171
GEOGRAPHICAL DISTRIBUTION OF ANIMALS 174
DISTRIBUTION OF ANIMALS IN TIME 180
SPECIAL ZOOLOGY 182
Phylum I. PROTOZOA 183
Class I. Rhizopoda 187
Order I. Monera 189
Order II. Lobosa 189
Order III. Heliozoa 190
Order IV. Radiolaria 192
Order V. Foraminifera 196
Order VI. Mycetozoa 198
Class II. Flagellata 200
Order I. Autoflagellata 200
Order II. Dinoflagellata 203
Order III. Cystoflagellata 203
Class III. Ciliata 204
Order I. Holotricha 209
Order II. Heterotricha 209
Order III. Peritricha 210
Order IV. Hypotricha 211
Order V. Suctoria 212
Class IV. Sporozoa 213
Order I. Gregarinida 213
Order II. Coccidiæ 215
Order III. Hæmosporida 216
Order IV. Myxosporida 217
Order V. Sarcosporida 218
SUMMARY 218
METAZOA 221
Phylum II. PORIFERA 221
Order I. Calcispongiæ 225
Order II. Silicispongiæ 226
SUMMARY 227
Phylum III. CŒLENTERATA 228
Class I. Hydrozoa 230
Order I. Hydraria 240
Order II. Hydrocorallinæ 241
Order III. Tubulariæ = Anthomedusæ 241
Order IV. Campanulariæ = Leptomedusæ 242
Order V. Trachomedusæ 242
Order VI. Narcomedusæ 242
Order VII. Siphonophora 243

PAGE
Class II. Scyphozoa 245
  Order I. Stauromedusæ 250
  Order II. Peromedusæ 250
  Order III. Cubomedusæ 250
  Order IV. Discomedusæ 250
Class III. Anthozoa 251
  Order I. Tetracoralla 258
  Order II. Octocoralla 258
  Order III. Hexacoralla 259
Class IV. Ctenophora 261
SUMMARY 265
Phylum IV. PLATHELMINTHES 267
Class I. Turbellaria 268
  Order I. Polycladidea 271
  Order II. Tricladidea 271
  Order III. Rhabdocœlida 271
Class II. Trematoda 271
  Order I. Polystomiæ 273
  Order II. Distomiæ 274
Class III. Cestoda 278
Class IV. Nemertini 289
SUMMARY 292
Phylum V. ROTIFERA 293
Phylum VI. CŒLHELMINTHES 295
Class I. Chætognathi 296
Class II. Nemathelminthes 298
  Order I. Nematoda 298
  Order II. Gordiacea 304
  Order III. Acanthocephala 304
Class III. Annelida 305
 Sub Class I. Chætopoda 306
  Order I. Polychætæ 311
  Order II. Oligochætæ 314
 Sub Class II. Gephyræa 316
  Order I. Chætiferi 317
  Order II. Inermes 317
  Order III. Priapuloidea 317
 Sub Class III. Hirudinei 318
  Order I. Gnathobdellidæ 321
  Order II. Rhynchobdellidæ 321
Class IV. Polyzoa 321
 Sub Class I. Entoprocta 321
 Sub Class II. Ectoprocta 322
Class V. Phoronida 325
Class VI. Brachiopoda 325
  Order I. Ecardines 328
  Order II. Testicardines 328
SUMMARY 328
Phylum VII. ECHINODERMA 329
Class I. Asteroidea 333

PAGE
Class II. Ophiuroidea 337
Class III. Crinoidea 338
Sub Class I. Eucrinoidea 342
Sub Class II. Edrioasteroidea 342
Sub Class III. Cystidea 342
Sub Class IV. Blastoidea 342
Class IV. Echinoidea 343
Order I. Palechinoidea 345
Order II. Cidaridæ 345
Order III. Clypeastroidea 346
Order IV. Spatangoidea 346
Class V. Holothuroidea 346
Order I. Actinopoda 349
Order II. Paractinopoda 349
SUMMARY 350
Phylum VIII. MOLLUSCA 351
Class I. Amphineura 356
Sub Class I. Placophora 356
Sub Class II. Solenogastres 358
Class II. Acephala 358
Order I. Protoconchiæ 365
Order II. Heteroconchiæ 367
Class III. Scaphopoda 369
Class IV. Gasteropoda 369
Order I. Prosobranchiata 378
Order II. Opisthobranchiata 381
Order III. Pulmonata 383
Class V. Cephalopoda 384
Order I. Tetrabranchia 394
Order II. Dibranchia 394
SUMMARY 395
Phylum IX. ARTHROPODA 398
Class I. Crustacea 408
Sub Class I. Trilobitæ 414
Sub Class II. Phyllopoda 415
Order I. Branchiopoda 416
Order II. Cladocera 417
Sub Class III. Copepoda 417
Order I. Eucopepoda 421
Order II. Siphonostomata 422
Sub Class IV. Ostracoda 422
Sub Class V. Cirripedia 423
Order I. Lepadidæ 425
Order II. Balanidæ 425
Order III. Rhizocephala 426
Sub Class VI. Malacostraca 426
Legion I. Leptostraca 427
Legion II. Thoracostraca 427
Order I. Schizopoda 428
Order II. Stomatopoda 429

PAGE
Order III. Decapoda 429
Order IV. Cumacia 437
Legion III. Arthrocostraca 438
Order I. Amphipoda 438
Order II. Isopoda 440
Class II. Acerata 442
Sub Class I. Gigantostraca 443
Order I. Xiphosura 444
Order II. Eurypterida 444
Sub Class II. Arachnida 444
Legion I. Arthrogastrida 447
Order I. Scorpionida 447
Order II. Phrynoidea 448
Order III. Microthelyphorida 448
Order IV. Solpugida 449
Order V. Pseudoscorpii 450
Order VI. Phalangida 450
Legion II. Sphærogastrida 451
Order I. Araneina 451
Order II. Acarina 453
Order III. Linguatulida 454
Tardigrada 455
Pycnogonida 456
Class III. Malacopoda 456
Class IV. Insecta 458
Sub Class I. Chilopoda 460
Sub Class II. Hexapoda 461
Order I. Apterygota 477
Order II. Archiptera 477
Order III. Orthoptera 480
Order IV. Neuroptera 481
Order V. Strepsiptera 483
Order VI. Coleoptera 483
Order VII. Hymenoptera 485
Order VIII. Rhynchota 489
Order IX. Diptera 491
Order X. Aphaniptera 493
Order XI. Lepidoptera 494
Class V. Diplopoda 496
SUMMARY 497
Phylum X. CHORDATA 501
Sub Phylum I. Leptocardii 502
Sub Phylum II. Tunicata 505
Order I. Copelatæ 506
Order II. Tethyoidea 508
Order III. Thaliacea 510
Sub Phylum III. Enteropneusta 512
Sub Phylum IV. Vertebrata 514
Series I. Ichthyopsida 555
Class I. Cyclostomata 555

PAGE
Sub Class I. Myzontes 556
Sub Class II. Petromyzontes 557
Class II. Pisces 557
Sub Class I. Elasmobranchii 569
Order I. Selachii 570
Order II. Holocephali 572
Sub Class II. Ganoidei 572
Order I. Crossopterygii 573
Order II. Chondrostei 573
Order III. Holostomi 573
Sub Class III. Teleostei 574
Order I. Physostomi 575
Order II. Pharyngognathi 576
Order III. Acanthopteri 577
Order IV. Anacanthini 577
Order V. Lophobranchii 578
Order VI. Plectognathi 578
Sub Class IV. Dipnoi 579
Class III. Amphibia 580
Order I. Stegocephali 586
Order II. Gymnophiona 587
Order III. Urodela 587
Order IV. Anura 588
Series II. Amniota 588
Class I. Reptilia 588
Order I. Theromorpha 594
Order II. Plesiosauria 594
Order III. Ichthyosauria 594
Order IV. Chelonia 594
Order V. Rhynchocephalia 595
Order VI. Dinosauria 595
Order VII. Squamata 596
Order VIII. Crocodilia 601
Order IX. Pterodactylia 602
Class II. Aves 603
Order I. Saururæ 612
Order II. Odontornithes 612
Order III. Ratitæ 612
Order IV. Carinatæ 613
Class III. Mammalia 617
Sub Class I. Monotremata 631
Sub Class II. Marsupialia 632
Order I. Polyprotodonta 633
Order II. Diprotodonta 633
Sub Class III. Placentalia 634
Order I. Edentata 635
Order II. Insectivora 636
Order III. Chiroptera 637
Order IV. Rodentia 638
Order V Ungulata 639

PAGE
Order VI. Proboscidia ... 643
Order VII. Hyracoidea ... 644
Order VIII. Sirenia ... 644
Order IX. Cetacea ... 645
Order X. Carnivora ... 646
Order XI. Prosimiæ ... 648
Order XII. Primates ... 649
SUMMARY ... 652

GENERAL PRINCIPLES OF ZOOLOGY.

INTRODUCTION.

Man's Relation to Other Animals.—The man who has learned to observe nature in a disinterested manner sees himself in the midst of a manifold variety of organisms, which in their structure, and even more in their vital phenomena, disclose to him a similarity to his own being. This similarity, with many of the mammals, especially the anthropoid apes, has the sharpness of a caricature. In the invertebrate animals it is softened; yet even in the lowest organisms, for our knowledge of which we are indebted to the microscope, it is still to be found: although here the vital processes which have reached such an astonishing complexity and perfection in ourselves can only be recognized in their simplest outlines. Man is part of a great whole, the Animal Kingdom, one form among the many thousand forms in which animal organization has found expression.

Purpose of Zoological Study.—If we would, therefore, fully understand the structure of man, we must, as it were, look at it upon the background which is formed by the conditions of organization of the other animals, and for this purpose we must investigate these conditions. To such endeavors the scientific knowledge of animal life, or Zoology, owes its origin and continued advancement. But meanwhile the subject of zoology has widened; for, apart from its relations to man, zoology has to explain the organization of animals and their relations to one another. This is a rich field for scientific activity; its enormous range is a consequence, on the one hand, of the well-nigh exhaustless variety of animal organization, and, on the other hand, of the different points of view from which the zoologist enters upon the solution of his problem.

In the first half of the last century the conception, which is still held by the public at large, was prevalent, if not quite universal, in scientific circles, that the aim of zoology is to furnish every animal with a name, to characterize it according to some easily recognizable features, and to classify it in a way to facilitate quick identification. By Natural History was understood the classification of animals, that is to say, only one part of zoology, indeed a part of minor importance, which can pretend to scientific value only when it is brought into relation with other problems (geographical distribution, evolution). This conception has during the past five decades become more and more subordinated. The ambition to describe the largest possible number of new forms and to shine by means of an extensive knowledge of species belongs to the past. In fact there is a tendency to undue neglect of classification. Morphology and Physiology to-day dominate the sphere of the zoologist's work.

Morphology, or the study of form, begins with the appearances of animals, and has first to describe all which can be seen externally, as size, color, proportion of parts. But since the external appearance of an animal cannot be understood without knowledge of the internal organs which condition the external form, the morphologist must make these accessible by the aid of dissection, of Anatomy, and likewise describe their forms and methods of combination. In his investigation he only stops when he has arrived at the morphological elements of the animal body, the cells. Everywhere the morphologist has to do with conditions of form: the only difference lies in the instruments by means of which he obtains his insight, according to whether he gathers his knowledge through immediate observation, or after a previous dissection with scalpel and scissors, or by use of the microscope. Therefore we cannot contrast Morphology and Anatomy, and ascribe to the former the description of only the external, and to the latter of only the internal parts. The distinction is not logically correct, since the kind of knowledge and the mental processes are the same in both cases. The distinction, too, is unnatural, since in many instances organs which in some cases lie in the interior of the body, and must be dissected out, belong in other cases to the surface of the body, and are accessible for direct description. Further, on account of their transparency the internal parts of many animals can be studied without dissection.

Comparative Anatomy.—For morphology, as for every science, the proposition is true that the mere accumulation of facts is not sufficient to give the subject the character of a science; an additional mental elaboration of this material is necessary. Such a result is reached by comparison. The morphologist compares animals with each other according to their structure, in order to ascertain what parts of the organization recur everywhere, what only within narrow limits, possibly restricted to the representatives of a single species. He thus gains a double advantage: (1) an insight into the relationships of animals, and hence the foundation for a Natural System; (2) the evidence of the laws which govern organisms. Any organism is not a structure which has arisen independently and which is hence intelligible by itself: it stands rather in a regular dependent relation to the other members of the animal kingdom. We can only understand its structure when we compare it with the closely and the more distantly related animals, e.g., when we compare man with the other vertebrates and with many lower invertebrate forms. Here we have to consider one of the most mysterious phenomena of the organic world, the path to the full explanation of which was first broken by the Theory of Evolution, as will be shown in another chapter.

Ontogeny.—To morphology belongs, as an important integral part, Ontogeny or Embryology. Only a few animals are completely formed in all their parts at the beginning of their individual existence; most of them arise from the egg, a relatively simple body, and then step by step attain their permanent form by complicated changes. The morphologist must, with the completest possible series, determine by observation the different stages, compare them with the mature animals, and with the structure and developmental stages of other animals. Here is revealed to him the same conformity to law which dominates the mature animals, and a knowledge of this conformity is of fundamental importance as well for classification as for the causal explanation of the animal form. The developmental stages of man show definite regular agreements, not only with the structure of the adult human being, which in and of itself would be intelligible, but also with the structure of lower vertebrates, like the fishes, and even with many of the still lower animals of the invertebrate groups.

Physiology.—In the same way as the morphologist studies the structure, the physiologist studies the vital phenomena of animals and the functions of their organs. Formerly life was regarded as the expression of a special vital force peculiar to organisms, and any attempt at a logical explanation of the vital processes was thereby renounced. Modern physiology has abandoned this theory of vital force; it has begun the attempt to explain life as the summation of extremely complicated chemico-physical processes, and thus to apply to the organic world those explanatory principles which prevail in the inorganic realm. The results obtained show that it is the correct method.

Since each organic form is the product of its development, since, further, the development represents to us the summation of most complicated vital processes, the explanation of the organic bodily form is, therefore, in ultimate analysis a physiological problem; though of course a problem whose solution lies still in the indefinitely distant future. What has been actually accomplished in this direction is only the smallest beginning, even in comparison with that which many falsely regard as already attained.

Biology.—According as the relations of each organism to the external world are brought about through its vital phenomena, there belongs to physiology, or at least is connected with it, the study of the conditions of animal existence, Œcology or Biology. This branch of the science has of late attained a very considerable importance. How animals are distributed over the globe, how climate and conditions influence their distribution, how by known factors the structure and the mode of life become changed, are questions which are to-day discussed more than ever before.

Paleontology.—Finally in the realm of zoology belongs also Paleozoology or Paleontology, the study of the extinct animals. For between the extinct and the living animals there exists a genetic relationship: the former are the precursors of the latter, and their fossil remains are the most trustworthy records of the history of the race, or Phylogeny. As in human affairs the present conditions can only be completely understood by the aid of history, so in many cases the zoologist must draw upon the results of paleontology for an explanation of the living animal world.

The science of zoology would be subdivided in the above-mentioned manner if we wished to proceed entirely on a scientific basis. Yet practical considerations have made many modifications necessary. On account of their paramount importance to the medical profession human anatomy and embryology have been raised to independent branches of science. In comparative physiology only the most general foundations have been laid; a more special physiology exists only for man and the higher vertebrates; this, too, for the above-named reasons has been made a special branch of science. Paleontology also has, in addition to its specific zoological tasks, attained importance as a scientific aid to geology, since it furnishes the materials for characterizing and fixing the various geological ages and the earth's history during those ages. When, therefore, at the present day we speak of zoology, we usually refer to *morphology and classification of living animals with consideration of their general vital phenomena.*

The views here given of the character of zoology have not been the same in all time. Like every science zoology has developed gradually; it has varied with each epoch and tendency, according as the systematic or the morphological or the physiological point of view was the prevailing one. It will now be interesting to take a hasty glance at the most important phases in the development of zoology. The reader will better understand the questions which now dominate zoological inquiry, if he know how these have arisen historically.

HISTORY OF ZOOLOGY.

Methods of Zoological Study.—In the history of zoology we can distinguish two great currents, which have been united in a few men, but which on the whole have developed independently, nay, more often in pronounced opposition to each other; these are on the one side the systematic, on the other the morphologico-physiological mode of studying animals. In this brief historical summary they will be kept distinct from one another, although in the commencement of zoological investigation there was no opposition between the two points of view, and even later this has in many instances disappeared.

Aristotle, the great Greek philosopher, has been distinguished as the Father of Natural History, which means that his predecessors' fragmentary knowledge of zoology could not be compared with the well-arranged order in which Aristotle had brought together his own and the previously existing knowledge of the nature of animals. In Aristotle favorable external conditions were united with more favorable mental ability. Equipped with the literary aid of an extensive library and the pecuniary means then more indispensable than now for natural-history investigation, he pursued the inductive method, the only one which is capable of furnishing secure foundations in the realm of natural science. It is a matter for great regret that there have been preserved only parts of his three most important zoological works, "Historia animalium," "De partibus," and "De generatione," works in which zoology is founded as a universal science, since anatomy and embryology, physiology and classification find equal consideration. How far Aristotle, notwithstanding many errors, attained to a correct knowledge of the structure and embryology of animals, is shown by the fact that many of his discoveries have been confirmed only within a century. Thus it was known to Aristotle, though only lately rediscovered by Johannes Müller, that many sharks are not only viviparous, but that also in their case the embryo becomes fixed to the maternal uterus and there is formed a contrivance for nutrition resembling the mammalian and even the human placenta; he knew the difference between male and female cephalopods, and that the young cuttlefish has a preoral yolk-sac.

The position which Aristotle took in reference to the classification of animals is of great interest; he mentions in his writings the very considerable number of about five hundred species. Since he does not mention very well-known forms, like the badger, dragonfly, etc., we can assume that he knew many more, but did not regard it necessary to give a catalogue of all the forms known to him, and that he mentioned them only if it was necessary to refer to certain physiological or morphological conditions found in them.

This neglect of the systematic side is further shown in the fact that the great philosopher is satisfied with two systematic categories, with *εἶδος*, species or kind, and *γένος* or group. His eight *γένη μέγιστα* would about correspond with the Classes of modern zoology; they have been the starting-point for all later attempts at classification, and may therefore be enumerated here:

1. Mammals (*ζῳοτοκοῦντα ἐν αὐτοῖς*).
2. Birds (*ὄρνιθες*).
3. Oviparous quadrupeds (*τετράποδα ᾠοτοκοῦντα*).
4. Fishes (*ἰχθύες*).
5. Molluscs (*μαλάκια*).
6. Crustaceans (*μαλακόστρακα*).
7. Insects (*ἔντομα*).
8. Animals with shells (*ὀστρακοδέρματα*).

Aristotle also noticed the close connexion of the first four groups, since he, without indeed actually carrying out the division, has contrasted the animals with blood, *ἔναιμα* (better, animals with red blood), with the bloodless, *ἄναιμα* (better, animals with colorless blood or with no blood at all).

DEVELOPMENT OF SYSTEMATIC ZOOLOGY.

Pliny.—It is a remarkable fact that after the writings of Aristotle, in which classification is much subordinated and only serves to express the anatomical relationships in animals, an exclusively systematic direction should have been taken. This is explicable only when we consider that the mental continuity of investigation was completely broken on the one hand by the decline and ultimate complete collapse of ancient classic civilization, and on the other by the triumphant advance of Christianity.

The decay of zoological investigation, that had only just begun to bloom, begins in the writings of Pliny. Although this Roman general and scholar was long lauded as the foremost zoologist of antiquity, he is now given the place of a not even fortunate compiler, who collected from the writings of others the accurate and the fabulous indiscriminately, and replaced the natural classification of animals according to structure by the unnatural, purely arbitrary division according to their place of abode (flying animals, land animals, water animals).

Zoology of the Middle Ages.—The rise of Christianity resulted in the complete annihilation of natural science and investigation. The world-renouncing character, which originally was peculiar to the Christian conception, led naturally to a disposition hostile to any mental occupation with natural things. Then came a time when answers to questions capable of solution by the simplest observation were sought by painstaking learned rummaging of the works of standard authors. How many teeth the horse has, was debated in many polemics, which would have led to bloodshed if one of the authors had not taken occasion to look into a horse's mouth. Significant of this mental bias which prevailed throughout the entire Middle Ages is the 'Physiologus' or 'Bestiarius,' a book from which the zoological authors of the Middle Ages drew much material. The book in its various editions names about seventy animals, among them many creatures of fable: the dragon, the unicorn, the phœnix, etc. Most of the accounts given of various animals are fables, intended to illustrate religious or ethical teachings. In a similar way the religious element played an important rôle in the many-volumed Natural History of the Dominican Albertus Magnus, and Vincentius Bellovacensis, and of the Augustine Thomas Cantimpratensis, although these used as a foundation for their expositions the Latin translation of Aristotle, the works of Pliny and other authors of antiquity.

Wotton.—Under such conditions we must regard it as an important advance that at the close of the Middle Ages, when the interest in scientific investigation awoke anew, Aristotle's conceptions were taken up and elaborated from a scientific standpoint. In this sense we can call the Englishman Wotton the successor of Aristotle. In 1552 he published his work "De differentiis animalium," in which he essentially copied the system of Aristotle, except that he admitted the new group of plant-animals or zoophytes. However, the title, 'On the Distinguishing Characters of Animals,' shows that of the rich treasury of Aristotelian knowledge the systematic results obtained the chief recognition, and thus Wotton's work inaugurated the period of systematic zoology, which in the Englishman Ray, but even more in Linnæus, has found its most brilliant exponents.

Linnæus, the descendant of a Swedish clergyman, whose family name Ingemarsson had been changed after a linden-tree near the parsonage, to Lindelius, was born in Rashult in 1707. Pronounced by his teachers to be good for nothing at study, he was saved from the fate of learning the cobbler's trade through the influence of a physician, who recognized the fine abilities of the boy, and won him for medical studies. He studied at Lund and Upsala; at the age of twenty-eight he made extended tours on the Continent, and at that time gained recognition from the foremost men in his profession. In 1741 he became professor of medicine in Upsala, some years later professor of natural history. He died in 1778.

Improvement of Zoological Nomenclature by Linnæus.—Linnæus's most important work is his "Systema Naturæ," which, first appearing in 1735, up to 1766–68 passed through twelve editions; after his death there came out a thirteenth, edited by Gmelin. This has become the foundation for systematic zoology, since it introduces for the first time (1) a sharper division into the system, (2) a definite scientific terminology, the binomial nomenclature, and (3) brief, comprehensive, clear diagnoses. In classification Linnæus employed four categories; he divided the entire Animal Kingdom into Classes, the Classes into Orders, these into Genera, the Genera finally into Species. The term Family was not employed in the "Systema Naturæ." Still more important was the *binomial nomenclature.* Hitherto the common names were in use in the scientific world, and led to much confusion; the same animals had different names, and different animals had the same names; in the naming of newly discovered animals there prevailed no generally accepted principle. This inconvenience was entirely obviated by Linnæus in the tenth edition of his Systema by the introduction of a scientific nomenclature. The first word, a noun, designates the genus to which the animal belongs, the following word, usually an adjective, the species within the genus. The names *Canis familiaris, Canis lupus, Canis vulpes,* indicate that the dog, wolf, and fox are related to one another, since they belong to the same genus, the genus of doglike animals, of which they are different species. Linnæus's method of naming was particularly valuable in the description of new species, inasmuch as it at the outset informed the reader to what position of relationship the new species was to be assigned.

In his characterization of the various systematic groups Linnæus broke completely with the hitherto-prevailing custom. His predecessors (as Gessner, Aldrovandus) in their Natural Histories had given a verbose and detailed description of each animal, from which the beginner was scarcely able to see what was specially characteristic for that animal, a matter which should have been emphasized in the definition. Linnæus, on the other hand, introduced brief diagnoses, which in a few words, never in sentence form, gave only what was necessary for recognition. Thus a way was found which insured comprehensibility in the enormously increasing number of known animals.

Influence of the Linnean System.—But in the great superiority of the Linnean System lay at the same time the germ of the one-sided development which zoology came to take under his influence. The logical perfecting of the system, which undoubtedly had become necessary, gave that a brilliant aspect, and hid the fact that classification is not the ultimate purpose of investigation, but only an important and indispensable aid to it. In the zeal for naming and classifying animals, the higher goal of investigation, knowledge of the nature of animals, was lost sight of, and the interest in anatomy, physiology, and embryology flagged.

From these reproaches we can scarcely spare Linnæus himself, the father of this tendency. For while in his "Systema Naturæ" he treated of a much larger number of animals than any earlier zoologist, he brought about no deepening of our knowledge. The manner in which he divided the animal kingdom, in comparison with the Aristotelian system, is rather a retrogression than an advance. Linnæus divided the animal kingdom into six classes: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. The first four classes correspond to Aristotle's four groups of animals with blood. In the division of the invertebrated animals into Insecta and Vermes Linnæus stands undoubtedly behind Aristotle, who attempted, and in part successfully, to set up a larger number of groups.

But in his successors, even more than in Linnæus himself, we see the damage wrought by the systematic method. The diagnoses of Linnæus were for the most part models, which, *mutatis mutandis,* could be employed for new species with little trouble. There was needed only some exchanging of adjectives to express the differences. With the hundreds of thousands of different species of animals there was no lack of material, and so the arena was opened for that spiritless zoology of species-making which in the first half of the last century brought zoology into such discredit. Zoology would have been in danger of growing into a Tower of Babel of species-describing had not a counterpoise been created in the strengthening of the physiologico-anatomical side.

DEVELOPMENT OF MORPHOLOGY.

Anatomists of Classic Antiquity.—Comparative anatomy—for this chiefly concerns us here—for a long time owed its development to the students of human anatomy; this is due to the fact that even up to a recent date comparative anatomy was assigned to the medical faculty, while zoology belonged to the philosophical faculty, as if it were an entirely separate study. The disciples of Hippocrates had previously studied animal anatomy for the purpose of obtaining an idea of human organization, from the structure of other mammals, and thus to gain a secure foundation for the diagnosis of human diseases. The work of classical antiquity most prominent in this respect, the celebrated Human Anatomy by Claudius Galenus (131–201 A.D.), is based chiefly upon observations upon dogs, monkeys, etc.; for in ancient times, and even in the Middle Ages, men showed considerable repugnance to making the human cadaver a subject of scientific investigation.

Middle Ages.—The first thousand years in which Christianity formed the ruling power in the mental life of the people was quite fruitless for anatomy; in the main men held to the writings of Galen and the works of his commentators, and seldom took occasion to prove their correctness by their own observations. With the ending of the Middle Ages the interest in independent scientific research first broke its bounds.

Vesal (1514–1564), the creator of modern anatomy, had the courage carefully to investigate the human cadaver and to point out numerous errors in Galen's writings which had arisen through the unwarranted application to human anatomy of the discoveries made upon other animals. By his corrections of Galen, Vesal was drawn into a violent controversy with his teacher, Sylvius, an energetic defender of Galen's authority, and with his renowned contemporary Eustachius, which did much for the development of comparative anatomy. At first animals were dissected only for the purpose of disclosing the cause of Galen's mistakes, but later through a zeal and love for facts. It was natural that first of all vertebrates found consideration, since they stand next to man in structure. Thus there appeared in the same century with Vesal's Human Anatomy drawings of skeletons of vertebrates by the Nuremberg physician Coiter; the anatomical writings of Fabricius ab Aquapendente, etc.

Beginning of Zootomy.—But later attention was turned also to insects and molluscs, indeed even to the marine echinoderms, cœlenterates, and Protozoa. Here, above all, three men who lived at the end of the seventeenth century deserve mention, the Italian Malpighi and the Dutchmen Swammerdam and Leeuwenhoek. The former's "Dissertatio de bombyce" was the pioneer for insect anatomy, since by the discovery of the vasa Malpighii, the heart, the nervous system, the tracheæ, etc., an extraordinary extension of our knowledge was brought about. Of Swammerdam's writings attention should be called particularly to "The Bible of Nature," a work to which no other of that time is comparable, since it contains discoveries of great accuracy on the structure of bees, May-flies, snails, etc. Leeuwenhoek, finally, was a most fortunate discoverer in the field of microscopic research, by him introduced into science. Besides other things he studied especially the minute inhabitants of the fresh waters, the 'infusion-animalcules,' a more careful investigation of which has led to a complete reversal of our conception of the essentials of animal organization.

The Dawn of Independent Observation.—The great service of the men named above consists chiefly in that they broke away from the thraldom of book-learning and, relying alone upon their own eyes and their own judgment, regained what had been lost, the blessing of independent and unbiassed observation. They spread the interest in observation of nature over a wide circle so that in the eighteenth century the number of independent natural-history writings had increased enormously. There were busy with the study of insect structure and development, de Geer in Sweden, Réaumur in France, Lyonet in Belgium, Rösel von Rosenhof in Germany; the latter besides wrote a monograph on the indigenous batrachia, which is still worth reading. The investigation of the infusoria formed a favorite occupation for the learned and the laity, as Wrisberg, von Gleichen-Russwurm, Schäffer, Eichhorn, and O. F. Müller. In most of the writings the religious character of the contemplations of nature are extraordinarily emphasized, and since we find that among these writers numerous clergymen (Eichhorn in Danzig, Gœze in Quedlinburg, Schäffer in Regensburg) attained distinction, we have a sign that a reconciliation had taken place between Christianity and natural science. As a criterion of the progress made in comparison with the earlier centuries, a mere glance at the illustrations is sufficient. Any one will at the first glance recognize the difference between the shabby drawings of an Aldrovandus and the masterly figures of a Lyonet or a Rösel von Rosenhof.

Period of Comparative Anatomy.—Thus through the zeal of numerous men filled with a love of nature a store of anatomical facts was collected, which needed only a mental reworking; and this mental reworking was brought about, or at least entered upon, by the great comparative anatomists who lived at the end of the eighteenth and the beginning of the nineteenth century. Among these the French zoologists Lamarck, Savigny, Geoffroy St. Hilaire, Cuvier, and the Germans Meckel and Goethe are especially to be named.

Correlation of Parts.—When the various animals were compared with one another with reference to their structure there was obtained a series of important fundamental laws, particularly the law of the Correlation of Parts and the law of the Homology of Organs. The former established the fact that there exists a dependent relation between the organs of the same animal, that local changes in one single organ also lead to corresponding changes at some distant part of the body, and that therefore from the constitution of certain parts an inference can be drawn as to the constitution of another part of the body. Cuvier particularly made use of this principle in reconstructing the form of extinct animals.

Homology and Analogy.—Still more important was the theory of the Homology of Organs. In the organs of animals a distinction was drawn between an anatomical and a physiological character; the anatomical character is the sum of all the anatomical features, as found in form, structure, position, and mode of connection of organs; the physiological character is their function. Anatomically similar organs in closely related animals will usually have the same functions, as, for example, the liver of all vertebrates has the function of producing gall; here anatomical and physiological characteristics go hand in hand. But this need not necessarily be the case; very often it may happen that one and the same function is possessed by organs anatomically different; as, for example, the respiration of vertebrates is carried on in fishes by gills, in mammals by lungs. Conversely, anatomically similar organs may have different functions, as the lungs of mammals and the swim-bladder of fishes; similar organs may also undergo a change of function from one group to another; the hydrostatic apparatus of fishes has come to be the seat of respiration in the mammals. Organs with like functions — physiologically equivalent organs — are called 'analogous'; organs of like anatomical constitution—anatomically equivalent organs—are called 'homologous.' It is the task of comparative anatomy to discover in the various parts of animals those which are homologous, i.e. those anatomically equivalent, and to follow the changes in them conditioned by a change of function.

Cuvier.—The foremost representative of comparative anatomy was Georges Dagobert Cuvier. He was born in 1769 in the town of Mömpelgardt (Montbeillard), then belonging to Würtemberg, and obtained his early training in the Karlschule at Stuttgart, where, through the influence of his teacher Kielmeyer, he was led to the study of comparative anatomy. The opportunity of going to the seashore which was offered to him as private instructor to Count d'Héricy he employed for his epoch-making investigations upon the structure of molluscs. In 1794, upon the persuasion largely of the man who afterwards became his great opponent, Geoffroy St. Hilaire, he moved to Paris, where he was made at first Professor of Natural History in the central school and in the College of France, later Professor of Comparative Anatomy in the Jardin des Plantes. As a sign of the great regard in which Cuvier was held, it should be noticed that he was repeatedly intrusted with high educational positions and was made a French peer. As such he died in 1832.

Type Theory.—Cuvier's investigations, apart from the molluscs, extended to the cœlenterates, arthropods, and vertebrates, living and fossil. He collected his extensive observations into his two chief works "Le règne animal distribué d'après son organization" and "Leçons d'anatomie comparée." Of quite epoch-making importance was his little pamphlet "Sur un rapprochement à établir entre les différentes classes des animaux," in which he founded his celebrated type theory, and which in 1812 introduced a complete reform of classification. The Cuvierian division, which has become the starting-point for all later classifications, differed, broadly speaking, from all the earlier systems in this, that the classes of mammals, birds, reptiles, and fishes were brought together into a higher grade under the name, introduced by Lamarck, of 'vertebrate animals'; that further the so-called 'invertebrate animals' were divided into three similar grades, each equal to that of the vertebrate animals, viz., Mollusca, Articulata, and Radiata. Cuvier called these grades standing above the classes, provinces or chief branches (*embranchements*), for which later the name Types was introduced by Blainville. But still more important are the differences which appear in the structural basis of the system. Instead of, like the earlier systematists, using a few external characteristics for the division, Cuvier built upon the totality of internal organization, as expressed in the relative positions of the most important organs, especially the position of the nervous system, as determining the arrangement of the other organs. "The type is the relative position of parts" (von Baer). Thus for the first time comparative anatomy was employed in the formation of a natural system of animals.

Lastly the type theory established an entirely new conception of the arrangement of animals. Cuvier found prevalent the theory that all animals formed a single connected series ascending from the lowest infusorian to man; within this series the position of each animal was definitely determined by the degree of its organization. On the other hand Cuvier taught that the animal kingdom consisted of several co-ordinated unities, the types, which exist quite independently side by side, within which again there are higher and lower forms. The position of an animal is determined by two factors: first, by its conformity to a type, by the structural plan which it represents; second, by its degree of organization, by the stage to which it attains within its type.

Comparative Embryology.—Evolution vs. Epigenesis.—The same results which Cuvier reached by the way of comparative anatomy were attained two decades later by C. E. von Baer by the aid of embryology. Embryology is the youngest branch of zoology. What Aristotle really knew, what was written by Fabricius ab Aquapendente and Malpighi upon the embryology of the chick, did not rise above the range of aphorisms, and were not of sufficient value to make a science. The difficulties of observation, due to the delicacy and the minuteness of the developmental stages, were lessened by the invention of the microscope and microscopical technique. Further, the prevailing philosophical conceptions placed hindrances in the way; there was no belief in Embryology in the present sense of the word; each organism was thought to be laid down from the first complete in all its parts, and only needed growth to unfold its organs (*evolutio* *); either the spermatozoon must be the young creature which found favorable conditions for growth in the store of food in the egg, or the egg represents the individual and was stimulated to the 'evolutio' by the spermatozoon. This theory led to the doctrine of inclusion, which taught that in the ovary of Eve were included the germs of all human beings who have lived or ever will live.

---

* This original meaning of 'evolution' is different from that prevailing at present.

Caspar Friedrich Wolff combated this idea with his "Theoria generationis" (1759); he sought to prove by observation that the hen's egg at the beginning is without any organization, and that gradually the various organs appear in it. In the embryo there is a new formation of all parts, an *Epigenesis*. This first assault upon the evolutionist school was entirely without result, chiefly because Albrecht von Haller, the most celebrated physiologist of the eighteenth century, by his influence suppressed the idea of epigenesis. Wolff was not able to establish himself in scientific circles in Germany, and was obliged to emigrate to Russia. Only after his death did his writings find, through Oken and Meckel, proper recognition.

Von Baer.—Thus it remained for Carl Ernst von Baer in his classic work, "Die Entwicklung des Hühnchens, Beobachtung und Reflexion" (1832), to establish embryology as an independent study. Baer confirmed Wolff's doctrine of the appearance of layerlike Anlagen, from which the organs arose; and on account of the accuracy with which he proved this he is considered the founder of the *germ-layer theory*. Further, he came to the conclusion that each type had not only its peculiar structural plan, but also its peculiar course of development; that for vertebrates an evolutio bigemina was characteristic, for the articulates the evolutio gemina, for the molluscs the evolutio contorta, and for the radiates the evolutio radiata. Here we meet for the first time the idea that for the correct solution of the questions of relationship of animals, and therefore a basis for a natural classification, comparative embryology is indispensable; an idea which in recent years has proved exceedingly fruitful.

Cell Theory.—Of fundamental importance for the further growth of comparative anatomy and embryology was the proof that all organisms, as well as their embryonic forms, were composed of the same elements, the cells. This knowledge is the quintessence of the cell theory, which during the third decade of the last century was advanced by Schleiden and Schwann, and which two decades later was completely remodelled by the protoplasm theory of Max Schultze. In the cell theory a simple principle of organization was found for all living creatures, for highly and for lowly organized plants and animals, and the wide realm of histology was laid open for scientific treatment.

REFORM OF THE SYSTEM.

Foundation of Modern Zoology.—With the establishment of comparative anatomy and embryology and the application of these to classification, and with the development of the cell theory and of histology, which is connected with it, we may say that the foundation of zoology was laid. Wonderful advances were made in vertebrate anatomy by the classic researches of Owen, Johannes Müller, Rathke, Gegenbaur, and others; our conceptions of organization have been completely altered by the work of Dujardin, Max Schultze, Haeckel, and others, who have proved the unicellularity of the lowest animals. The germ-layer theory was further elaborated by Remak and Kölliker; and applied to the invertebrate animals by Kowalewsky, Haeckel, and Huxley. It is beyond the limits of this brief historical summary to go into what has been accomplished in regard to the other branches of the animal kingdom; it must here be sufficient to mention the most important changes which the Cuvierian system has undergone under the influence of increasing knowledge.

The Division of the Radiata.—Of the four types of Cuvier the branch Radiata was undoubtedly the one of whose representatives he had the least knowledge; it was therefore the least natural, since it comprised, besides the radially symmetrical cœlenterates and echinoderms, other forms, which, like the worms, were bilaterally symmetrical, or, like many infusorians, were asymmetrical. Thus it came about that most reforms have here found their point of attack.

C. Th. von Siebold was the originator of the first important reform. He limited the type Radiata, or, as he termed them, the *Zoophytes,* to those animals with radially symmetrical structure (Echinoderms and the Plant-animals); separating all the others, he formed of the unicellular organisms the branch of 'primitive animals' or Protozoa; the higher organized animals he grouped together as worms or Vermes; at the same time he transferred a part of the Articulata, the annelids, to the worm group, and proposed for the other articulates, crabs, millipedes, spiders, and insects, the term Arthropoda.

Leuckart, about the same time (1848), divided the branch

Radiata into two branches differing greatly in structure. The lower forms, in which no special body-cavity is present, the interior of the body consisting only of a system of cavities serving for digestion, the alimentary canal, he called the Cœlentera (essentially the Zoophyta of the older zoologists); to the rest, in which the alimentary canal and the body-cavity occur as two separate cavities, he gave the name Echinoderma.

The Present System.—Thus there resulted seven classes: Protozoa, Cœlentera, Echinoderma, Vermes, Arthropoda, Mollusca, and Vertebrata. Still this arrangement does not meet the requirements of a natural system and hence is more or less unsatisfactory. Some zoologists are returning to the Cuvierian classification to the extent of uniting the segmented worms with the arthropods in a group Articulata. Upon the ground of important anatomical and embryological characters the Brachiopoda, the Bryozoa, and the Tunicata have been separated from the Mollusca; they form the subject of diverse opinions. The relationships of the first two groups have not yet been settled: of the Tunicata we know indeed that they are related to the Vertebrata, but the differences are such that they cannot be included in that group. The only way out of the difficulty is to unite vertebrates, tunicates, and some other forms in a larger division, Chordata. The Vermes, too, must be divided, as will appear in the second part of this volume.

HISTORY OF THE THEORY OF EVOLUTION.

Importance of the Subject.—Before closing the historical introduction we must consider the historical development of a question whose importance might, on a superficial examination, be underrated, but which from a small beginning has grown into a problem completely dominating zoological research, and has occupied not only zoologists, but all interested in science generally. This is the question of the logical value of the systematic conceptions species, genus, family, etc.

The Nature of Species.—In nature we find only separate animals: how comes it that we classify them into larger and smaller groups? Are the single species, genera, and the other divisions which the systematist distinguishes, fixed quantities, as it were fundamental conceptions of nature, or a Creator's thoughts, which find expression in the single forms? Or are they abstractions which man has brought into nature for the purpose of making it comprehensible to his mental capabilities? Are the specific and generic names only expressions which have become necessary, from the nature of our mental capacity, for the gradation of relationship in nature, which in and for themselves are not immutable, and hence can undergo a gradual change? Practically speaking, the problem reads: are species constant or changeable? What is true for species must necessarily be true for all other categories of the system, all of which in the ultimate analysis rest upon the conception of species.

Ray's Conception of Species.—One of the first to consider the conception of species was Linnæus's predecessor, the Englishman John Ray. In the attempt to define what should be understood as a species he encountered difficulties. In practice, animals which differ little in structure and appearance from one another are ascribed to the same species; this practical procedure cannot be carried out theoretically; for there are males and females within the same species which differ more from one another than do the representatives of different species. Thus John Ray reached the genetic definition when he said: for plants there is no more certain criterion of specific unity than their origin from the seeds of specifically or individually like plants; that is to say, generalized for all organisms: to one and the same species belong individuals which spring from similar ancestors.

The 'Cataclysm Theory.'—With Ray's definition an entirely uncontrollable element was brought into the conception of species, since no systematist usually knew anything, nor indeed could he know anything, as to whether the representatives of the species placed before him sprang from similar parents. It was therefore only natural that the conception of species put on a religious garb, since by resting upon theological ideas it found a firmer support. Linnæus said: "Tot sunt species quot ab initio creavit infinitum Ens"; with this he built up a conception of species upon the tradition of the Mosaic history of creation, a procedure quite unjustified upon grounds of natural science, since it drew one of its fundamental ideas from transcendental conceptions, not from the experience of natural science. Linnæus's definition showed itself untenable, as soon as paleontology began to make accessible a vast quantity of extinct animals deposited as fossils. With an odd fancy, the fossils, being inconvenient for study, were for a long time regarded as outside the pale of scientific research. They might be sports of nature, it was said, or remains of the Flood, or of the influence of the stars upon the earth, or products of an *aura* *seminalis*, a fertilizing breath, which, if it fell upon organic bodies, led to the formation of animals and plants, but if it strayed upon inorganic materials gave rise to fossils. The foundation of scientific paleontology by Cuvier put an end to such empty speculations. Cuvier proved beyond a doubt that these fossils were the remains of animals of a previous time. Just as the formation of the earth's crust by successive overlying layers made possible the recognition of different periods in the earth's history, so paleontology taught how to recognize also the different periods in the vegetable and animal world of life on our globe. Each geological age was characterized by a special world of animals quite peculiar to it; and these animal worlds differed the more from the present, the older the period of the earth to which they belonged. All these generalizations led Cuvier to his cataclysm theory, that a great revolution brought each period of the earth's history to an end, destroying all life, and that upon the newly formed virgin earth a new organic world of immutable species sprang up.

Objections to the Cataclysm Theory.—By the supposition of numerous acts of creation the Linnean conception of species seemed to be rescued, though, to be sure, by summoning to its aid hypotheses which had neither foundation in science nor justification in theology. The logical results of Cuvier's cataclysm theory were conceptions of a Creator who built up an animal world only for the purpose of destroying it after a time as a troublesome toy; it has therefore at no time found warm supporters, at least among geologists, for whom it was intended. Of the prominent zoologists there is only to be mentioned Louis Agassiz, who till the end of his life remained faithful to this theory.

Under these conditions it is readily understood how thinking naturalists, who felt the necessity of explaining the character of organic nature simply and by a natural law capable of general application, began to doubt the fixity of species, and were led to the theory of change of form, the Theory of Descent, or Evolution.

Darwin's Predecessors.—Even in Cuvier's time there prevailed a strong current in favor of this theory. It found expression in England in the writings of Erasmus Darwin (grandfather of the renowned Charles Darwin); in Germany in the works of Goethe, Oken, and the disciples of the 'natural philosophical' school; in France the genealogical theory was developed particularly by Buffon, Geoffroy St. Hilaire, and Lamarck. Its completest expression was found in Lamarck's "Philosophie zoologique" (1809); its arguments will be considered in the following paragraphs.

Lamarck (Jean Baptiste de Monet, Chevalier de Lamarck, born in Picardy, 1744, died, Professor at the Jardin des Plantes, 1829) taught that on the earth at first organisms of the simplest structure arose in the natural way through spontaneous generation from non-living matter. From these simplest living creatures have developed, by gradual changes in the course of an immeasurably vast space of time, the present species of plants and animals, without any break in the continuity of life upon our globe; the terminal point of this series is man; the other animals are the descendants of those forms from which man has developed. Lamarck, in accordance with the then prevailing conceptions, regarded the animal kingdom as a single series grading from the lowest primitive animal up to man. Among the causes which may influence the change and perfecting of organisms, Lamarck emphasized particularly *use* and *disuse;* the giraffe has obtained a long neck because by a special condition of life he was compelled to stretch, in order to browse the leaves on high trees; conversely, the eyes of animals which live in the dark have degenerated from lack of use into functionless structures. The direct influence of the external world must be unimportant; the changes in the surroundings (Geoffroy St. Hilaire's *le monde ambient*) must for the most part act indirectly upon animals by altering the conditions for the use of organs.

Evolution vs. Creation.—Lamarck's ingenious work remained almost unnoticed by his contemporaries. On the other hand there arose a violent controversy between the defenders and the opponents of the evolution theory when [1830] Geoffroy St. Hilaire in a debate in the Academy at Paris defended against Cuvier the thesis of a near relationship of the vertebrates and the insects, and set up the proposition that the latter were "vertebrates running on their backs." The conflict ended in the complete overthrow of the theory of evolution; the defeat was so complete that the problem vanished for a long time from scientific discussion, and the theory of the fixity of species again became dominant. This error was occasioned by many causes. Above all, the theory of Geoffroy St. Hilaire and Lamarck was rather a clever conception than founded on abundant facts; besides, it had in it as a fundamental error the doctrine of the serial arrangement of the animal world. Opposed to this stood Cuvier's great authority and his extensive knowledge, the latter making it easy for him to show that the animal kingdom was made up of separate co-ordinated groups, the types.

Lyell.—In the same year in which Cuvier obtained his victory over Geoffroy St. Hilaire, his theory of the succession of numerous animal worlds upon the globe received its first destructive blow. Cuvier's cataclysm theory had two sides, a geological and a biological. Cuvier denied the continuity of the various terrestrial periods, as well as the continuity of the fauna and flora belonging to them. In 1830–32 appeared the "Principles of Geology" by Lyell, an epoch-making work, which, in the realm of geology, completely set aside the cataclysm theory. Lyell proved that the supposition of violent revolutions on the earth was not necessary in order to explain the changes of the earth's surface and the superposition of its strata; that rather the constantly acting forces, elevations and depressions, the erosive action of water, be it as ebb and flow of the tide, as rain, snow, or ice, or as the flow of rivers and brooks rushing as torrents towards the sea, are sufficient to furnish a complete explanation. Very gradually in the course of a vast space of time the earth's surface has changed, and passed from one period into the next, and still at the present day the constant process of change is going on. The continuity in the geological history of the earth, here postulated for the first time, has since then become one of the fundamental axioms of Geology; on the other hand the discontinuity of living creatures, although the geological support of this was frail, was for a long time regarded as correct.

Darwin.—It is the great merit of Charles Darwin that he took up the theory of descent anew after it had rested a decade, and later brought it into general recognition. With this began the most important period in the history of zoology, a period in which the science not only made such an advance as never before, but also began to obtain a permanent influence upon the general views of men.

Charles Darwin was born at Shrewsbury, Eng., in 1809. After studying at the universities of Edinburgh and Cambridge, he joined as naturalist the English war-ship "Beagle." In its voyage from 1831 to 36 around the globe, Darwin recognized the peculiar character of island faunas, particularly of the Galapagos Islands, and the remarkable geological succession of edentates in South America; these facts formed for him the germ of his epoch-making theory. Further results of this journey were his beautiful monograph on the Cirripedia, and the classic investigation of coral-reefs. After his return to England Darwin lived, entirely devoted to scientific work, chiefly in the hamlet of Down, county Kent, up to the time of his death in 1882. He was incessantly busy in developing his conception of the origin of species, and in collecting for this a constantly increasing array of facts. The first written notes, the fundamental ideas of which he communicated to friends, particularly the geologist Lyell and the botanist Hooker, were made in 1844, but the author was not persuaded to give them publicity. Not until 1858 did Darwin decide to make his first contribution to science. In this year he received an essay sent by the traveller Wallace, which in its most important points coincided with his own views. At the same time with Wallace's manuscript an abstract of Darwin's theory was published. In the next year (1859) appeared the most important of his writings, "On the Origin of Species by means of Natural Selection," and in rapid succession a splendid series of works, the fruit of many years of preparatory labors. For the history of the theory the most important of these are: (1) "Upon the Variation of Plants and Animals under Domestication," two volumes, which chiefly contain a collection of material for proofs; (2) on "The Descent of Man," a work which gives the application of the theory to man.

No scientific work of this century has attracted so much attention in the zoological, we may even say in the whole educated world, as "The Origin of Species." It was generally received as something entirely new, so completely had the scientific tradition been lost. In professional circles it was stoutly combated by one faction, with another it found well-wishing but hesitating acceptance. Only a few men placed themselves from the beginning in a decided manner on the side of the great British investigator. There was a lively scientific battle, which ended in a brilliant victory for the theory of evolution. At the present time all our scientific thoughts are so permeated with the idea of evolution that we can scarcely speak of any considerable opposition to it.

Post-Darwinian Writers.—Among the men who have most influenced this rapid advance is to be mentioned, besides A. R. Wallace, the co-founder of Darwinism, above all Ernst Haeckel, who in his "General Morphology" and his "Natural History of Creation" has done much towards the extension of the theory. Among other energetic defenders of the theory in Germany should be mentioned Fritz Müller, Carl Vogt, Weismann, Moritz Wagner, and Nägeli, even if they have taken special standpoints in reference to the causes conditioning the changes of form. Among the English naturalists are to be named particularly Huxley, Hooker, and Lyell. In America Gray, Cope, and Hyatt were early supporters. Darwinism was long in obtaining an entrance into France.

DARWIN'S THEORY OF THE ORIGIN OF SPECIES.

Before Darwin wrote the idea of fixity of species prevailed among systematists. It was recognized that all the individuals of a species are not alike, and that more or less pronounced variability occurs, so that it was possible to distinguish races and varieties within the species, but it was believed that the variations never transcended specific bounds.

The Problem Stated.—Darwin begins with a criticism of the term species. Is the conception of species on the one side and that of race and variety on the other something entirely different? Are there special criteria for determining beyond the possibility of a doubt whether in a definite case we have to do with a variety of a species or with a different species? or do the conceptions in nature pass into one another? Are species varieties which have become constant, and precisely in the same manner are varieties species in the process of formation?

Morphological Characters.—A. *Distinction between Species and Variety.*—For the settlement of this fundamental question morphological and physiological characters can be considered. In the practice of the systematists usually the morphological characters prevail exclusively; for that reason they will be here considered first. If, among a great number of forms similar to one another, two groups can be adduced which differ considerably from one another, if the difference between them be obliterated by no intermediate forms, and if in several successive generations they remain constant, then the systematist speaks of a 'good species'; on the other hand he speaks of varieties of the same species when the differences are slight and inconstant, and when they lose their importance through the existence of intermediate forms. A definite application of this rule discloses great incongruities, many animal and vegetable groups being regarded by one set of systematists as good species, by another only as 'sports,' i.e., as varieties of the same species. The differences between the 'sports' of our domestic animals are in many instances so considerable that formerly they were regarded not only as sufficient for the foundation of good species, but even of genera and families. In the fantail pigeon the number of tail-feathers, formerly only 12–14, has increased to 30–42 (fig. 1c); among the other races of pigeons enormous variations are found in the size of the beak and feet in comparison with the rest of the body (figs. 1A, 1B); even the skeleton itself participates in this variation, as is shown by the fact that the total number of vertebræ varies from 38 (in the carrier-pigeon) to 43 (in the pouter), the number of sacral vertebræ from 14 to 11.

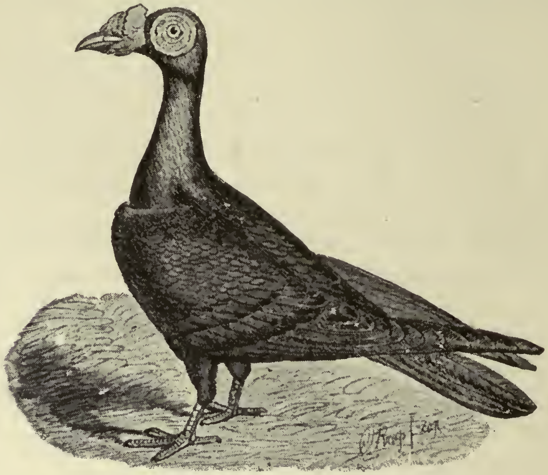


FIG. 1A.—English carrier-pigeon. (After Darwin.)

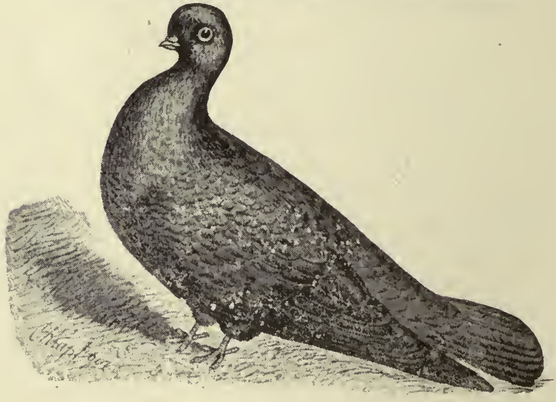


FIG. 1B.—English tumbler-pigeon. (After Darwin.)

B. *Variation within the Species.*—Now in respect to the occurrence of transitional forms and the constancy of differences, there is within one and the same 'good species' the greatest conceivable difference. In many very variable species the extremes are united by many transitions; in other cases sharply circumscribed groups of forms, or races, can be distinguished within the same species. In the race, the peculiar characteristics are inherited from generation to generation with the same constancy as in good species. This is shown in the human races, and in many pure, cultivated races of domesticated animals.

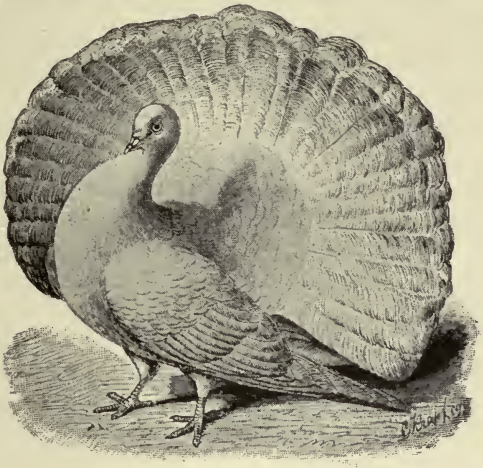


FIG. 1C.—English fantail pigeon. (After Darwin.)

Physiological Characters.—A. *Crossing of Species and Varieties.*—A critical examination leads to the conclusion that Morphology is indeed useful for grouping animals into species and varieties, but that it leaves us completely in the lurch when it is called upon to show the distinctions between what should be called a species and what a variety. Therefore there remains open to the systematist only one resource, i.e., to summon Physiology to his aid. This has been done, and it has disclosed considerable distinctions in reproduction. We should expect *a priori* that the individuals of different species would not reproduce with each other; on the other hand under normal conditions the individuals of one and the same species, even though they are of different varieties or races, should be entirely fertile. One must beware of arguing in a circle in proof of these two propositions; it would be an argument in a circle if an experimenter should regard two animals as representatives of one species only because they proved to be fertile together, while under their former relations he assigned them to different species. Rather the question for him must read: does physiological experiment lead to the same systematic distinctions as does the common systematic experience, viz., the depreciation of constancy and the divergence of distinguishing characters?

B. *The Intercrossing of Species.*—This field is as yet far from being sufficiently investigated experimentally; yet some general propositions can be set up: (1) that not a few so-called 'good species' can be crossed with one another; (2) that in general the difficulty of crossing increases, the more distant the systematic relationship of the species used; (3) that these difficulties are by no means directly proportional to the systematic divergence of the species. The most favorable material for research is furnished by those animals in which artificial fertilization can be carried out, i.e., of which one can take the eggs and spermatozoa and mix them independently of the will of the animals. Thus hybrids have been obtained from species which belong to quite different genera, while very often nearly-related species will not cross. Among fishes we know hybrids of *Abramis brama* and *Blicca björkna*, of *Trutta salar* (salmon) and *Trutta fario* (trout); among sea-urchins the spermatozoa of *Strongylocentrotus lividus* fertilize with great readiness the eggs of *Echinus microtuberculatus*, but only rarely the eggs of *Sphærechinus granularis*, which is nearer in the system. It also happens that crossing in one direction (male of A and female of B) is easily accomplished, but in the other direction (male of B and female of A) it completely fails; as, for example, the sperm of *Strongylocentrotus lividus* fertilizes well the eggs of *Echinus microtuberculatus*, but, conversely, the sperm of *E. microtuberculatus* does not fertilize the eggs of *S. lividus*. Even better known is the fact that salmon eggs are fertilized by trout sperm but not trout eggs by salmon sperm. Eggs have been fertilized by sperm belonging to different families, orders, and possibly classes. Eggs of *Pleuronectes platessa* and *Labrus rupestris* by sperm of the cod (*Gadus morrhua*), frogs' eggs (*Rana arvalis*) by sperm of two species of *Triton*, eggs of a starfish (*Asterias forbesi*) by milt from a sea-urchin, *Arbacia pustulosa* (??). In these extreme cases, it is true, the hybrids die during or at the close of segmentation, before the embryo is outlined.

In the case of animals where copulation is necessary the difficulties of experimentation increase, since here often between males and females of different species there exists an aversion which prevents any union of the sexes. Yet in this case we know crosses of different species; among the vertebrates crossing takes place, e.g., between the horse and the ass; our domestic cattle and the zebu; ibex (or wild buck) and she-goat; sheep and goats; dog and jackal; dog and wolf; hare and rabbit (*Lepus darwini*); American bison and domestic cattle; etc.; among birds, between different species of finches and of grouse; mallard (*Anas boschas*) and the pintail duck (*Dafila acuta*); the European goose and the Chinese goose (*Anser ferus* and *A. cygnoides*). Among the insects, especially the Lepidoptera, the cases are many, but the resulting eggs produce larvæ of slight vital force only in the case of *Actias luna* and *A. isabellæ*.

C. *Fertility of Hybrids and Mongrels.*—Since many hybrids, as the mule, have been known for thousands of years, the criterion is, as it were, pushed back one stage; if the infertility in cases of crosses in many species is not immediately noticeable, yet it may be apparent in the products of the cross. While the products of the crossing of varieties, the 'mongrels,' always have a normal, often an increased, fertility, the products of the crossing of species, the hybrids, should always be sterile. But even this is a rule, not a law. The mule (which only very rarely reproduces) and many other hybrids are indeed sterile, but there are not a few exceptions, although the number of experiments in reference to this point is very small. Hybrids of hares and rabbits have continued fruitful for generations; the same is true of hybrids obtained from the wild buck and the domesticated she-goat; from *Anser cygnoides* and *A. domesticus;* from *Salmo salvelinus* and *S. fontinalis; Cyprinus carpio* and *Carassius vulgaris; Bombyx cynthia* and *B. arrindia*.

D. *Inbreeding.*—Even the second of the above statements, that individuals of a species, provided they are sound, always reproduce with one another, needs limitation. Breeders of animals have long known the disastrous consequences of inbreeding—that the reproductive power is reduced even to sterility if, for breeding, descendants of a single pair be continually chosen. Darwin has collected not a few cases where undoubted members of the same species have been completely sterile with one another; as certain forms of primrose and other di- and tri-morphic species. Examples of the sterility of mongrels are known only in botany (certain varieties of maize and mullein).

Conditions Governing Fertility in Sexual Reproduction.—When we look over these facts it would seem as if continued fertility in sexual reproduction were guaranteed by a not too considerable difference in the sexual products. Too great similarities, as these exist in inbreeding, and too great differences, as in the hybridization of different species, are injurious and are abhorred by Nature. Sexual reproduction possesses an optimum; if this be departed from in either direction, diminution gradually follows. But for that reason it has already been said that here gradual and not primary differences exist, and therefore this character cannot be employed as a primary distinction between species and varieties.

Difficulties in Classification.—The final result of all this discussion may be summed up as follows: up to the present time, neither by physiological nor by morphological evidence has there been successfully fixed in a clear and generally applicable way a criterion which can guide the systematist in deciding whether certain series of forms are to be regarded as good species or as varieties of a species. Zoologists are guided rather in practice by a certain tact for classification, which, however, in difficult cases leaves them in the lurch, and thus the opinions of various investigators vary.

Change of Varieties into Species.—The conditions above discussed find their natural explanation in the assumption that sharp distinctions between species and variety do not exist; that *species are varieties which have become constant, and varieties are incipient species.* The meaning of the above can be made clear by explanation of a concrete case. Individuals of a species begin to vary, i.e., compared with one another they attain a greater or less difference in character. So long as the extreme differences are bridged by transitional forms we speak of varieties of a species; if, on the other hand, the intermediate transitions have died out, and the differences have in the course of a long space of time become fixed, and so very much intensified that a sexual union of the extreme forms results either in complete sterility or at least in a marked tendency towards sterility, then we speak of different species.

Species may be Related to each other in Unequal Degrees.—In favor of this view, that varieties will in longer time become species, is the great agreement which in the large majority of cases exists between the two. In genera which comprise a remarkable number of species, the species usually show also many varieties; the species are then usually grouped in sub-genera, i.e., they are related to each other in unequal degrees, since they form small groups arranged around certain species. In regard to the varieties also the case is similar. In such genera the formation of species is in active progress; but each species formation presupposes a high degree of variability.

Phylogeny.—It is now clear that what has here been worked out in the case of the species must also apply to the other categories of the system. Just as by divergent development varieties become species, so must species by continued divergence become so far removed from one another that we distinguish them as genera. It will be only a question of time when these differences will become still greater, and cause the establishment of orders, classes, and branches, just as the tender shoots of the young plantlet become in the strong tree the chief branches from which spring lateral branches and twigs. If we pursue this train of thought to its ultimate consequences, we reach the conception that all the animals and plants living at present have arisen by means of variation from a few primitive organisms. Inasmuch as at least many thousands of years are required for the formation of several new species through the variability of one, there must then have been necessary for this historical development of the animal and vegetable kingdoms a space of time greater than our mental capacity can grasp. Since for the idea of the individual development (embryology) of an animal the term Ontogeny has been chosen, it has also proved convenient to apply to the historical development of animals—though this has not been observed, but only inferred—the term History of the Race or Phylogeny.

Spontaneous Generation.—If we attempt to derive all living animals from a common primitive form, we are compelled to assume that this was of extremely simple organization, that it was unicellular; for the simpler, the less specialized, the organization, so much the greater is its capacity for variation. Only from simple organisms can the lower unicellular organisms, the Protozoa, be derived. Finally, for the simple organisms alone can we conceive a natural origin. Since there was undoubtedly a time upon our earth when temperatures prevailed which made life impossible, life must at some time have arisen, either through an act of creation or in a natural way through spontaneous generation. If, in agreement with the spirit of natural science, we invoke for the explanation of natural facts only the forces of nature, we are driven to the hypothesis of spontaneous generation, namely, that by a peculiar combination of materials without life, the complicated mechanism which we call 'life' has arisen. This hypothesis also supposes that the first organisms possessed the simplest conceivable structure.

Variability not proven to be a Universal Principle.—Starting from a basis of facts, by generalization we reach a simple conception of the origin of the animal kingdom, but we have in equal measure departed from the results of direct observation. Observations only show us that species are capable of changes and can from themselves produce new species. That this capacity for variation is a universal principle, a principle which explains to us the origin of the animal world, needs further demonstration.

Proofs of Phylogeny.—The rise of the existing animal world is a process which has taken place in the thousands of years long past, but is no longer accessible for direct observation, and therefore it can never be proved in the sense that we explain the individual development of an organism. In regard to the conception of the simple evolution of animals we can merely prove the probability; yet it is shown that all our observations of accessible facts not only agree with this conception, but find in it their only simple explanation. Such facts are furnished to us by the classification of animals, paleontology, geographical distribution, comparative anatomy, and comparative embryology.

(*1*) *Proofs from Classification.*—For a long time it has been recognized, and in recent times finds ever-increasing confirmation, that if we wish to express graphically the relationships of animals, their classes, orders, genera, and species, simple co-ordination and subordination are not sufficient, but one must select a treelike arrangement, in which the principal divisions, more closely or distantly related to one another,—the branches, phyla, or types,—represent the main limbs, while the smaller branches and twigs correspond to the several classes, orders, etc. This is, in fact, the arrangement to which the theory of evolution, as seen above, necessarily leads.

(*2*) *Paleontological Demonstration* approaches nearest to what one might call direct proof; for paleontology gives us the only traces of existence which the predecessors of the present animal world have left. Even here a hypothetical element has crept into the demonstration. We can only observe that various grades of forms of an animal group are found in successive strata; if we unite these into a developmental series, and regard the younger as derived from the older by variation, we depart, strictly speaking, from the basis of fact. But the value of paleontological evidence is weakened much more by its extreme incompleteness. In fossils only the hard parts are generally preserved; the soft parts, on the other hand, which alone are present, or at least make up the most important part of many animals, are almost always lost. Only rarely are the soft parts (muscle of fishes, ink-bag of cephalopods, outlines of medusæ) preserved in the rocks. Even the hard parts remain connected only under exceptionally favorable conditions. If further we take into consideration the fact that these treasures are buried in the bosom of the earth, and are usually obtained only by accident, in quarrying and road-building, and besides only extremely seldom excavated with scientific care, it becomes sufficiently clear how little is to be expected from the past and indeed future material of paleontology.

Examples of Paleontological Proof.—Yet paleontology has already furnished many important proofs of the theory of descent. It has shown that the lower forms appeared first, and the more highly organized later. Among animals in general the latest to appear were the vertebrates, and of these the mammals; among the mammals man. For smaller groups genealogical material has

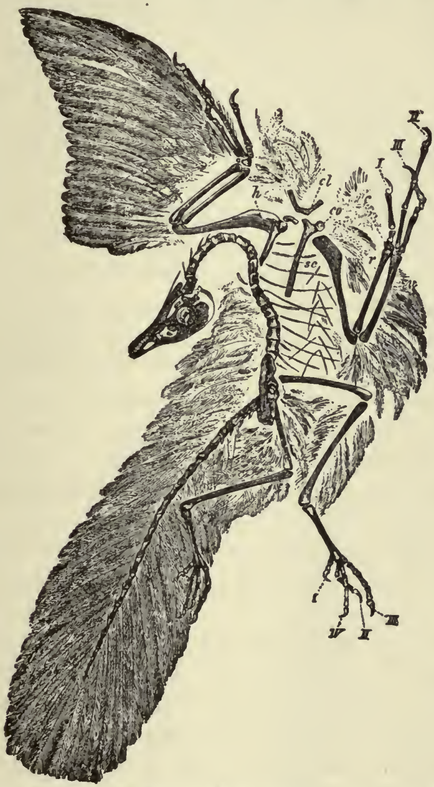


FIG. 2.—*Archæopteryx lithographica.* (After Zittel.) *cl*, clavicle; *co*, coracoid; *h*, humerus; *r*, radius; *u*, ulna; *c*, carpus; I–IV, digits; *sc*, scapula.

fortunately been found. Transitional forms connect the single-toed horse of the present with the four-toed *Eohippos* of the eocene; for all the hoofed animals a common starting-point or ancestral form has been found in the Condylarthra. Transitional forms have also been found between the greater divisions, as, e.g., between reptiles and birds, the remarkable toothed birds, and the *Archæopteryx* (fig. 2), a bird with a long, feathered, lizard-like tail.

(*3*) *Morphological Proofs.*—When we employ comparative anatomy and embryology in support of evolution, we find that the two studies have so many points in common that they can best be treated together.

Cuvier and von Baer taught that the separate types of the animal kingdom are units, each with a special structure and plan of development peculiar to it; farther, that there are no similarities in structure and in the development forming a bridge from type to type. The first of these two propositions is still regarded as correct, but the second, which alone is important for the theory of evolution, has become quite untenable. All animals have a common organic basis in the cell and are thereby brought close to one another; all multicellular animals agree in the principal points during the first stages of their development, during the fertilization, cleavage of the egg, and the formation of the first two germ-layers, and vary from one another only in such differences as may occur within one and the same type. Also the peculiarities which distinguish each type in structure and in the mode of development are not without intermediate phases. Especially from the branch of the worms there lead off transitional forms to the other branches: *Balanoglossus* to both echinoderms and chordates, the annelids and *Peripatus* to the arthropods, the tunicates and *Amphioxus* to the vertebrates. In some representatives of each type the structure and the mode of development are simpler, thereby approaching to the conditions which obtain in the other types. The existence of such transitional forms is one of the most important proofs *in favor* of the theory of evolution, and speaks *against* the assumption of a rigid unvarying type in Cuvier's sense.

Fundamental Law of Biogenesis.—A fact that weighs heavily in the balance in favor of the theory of evolution is the fact that the structure and mode of development of animals is ruled by a law which at present can only be explained by the assumption of a common ancestry. Each animal during its development passes through essentially the stages which remain permanent in the case of lower or at least more primitive animals of the same branch, as the three following examples will show: (1) In the early stages of development the human embryo (fig. 3) possesses remarkable

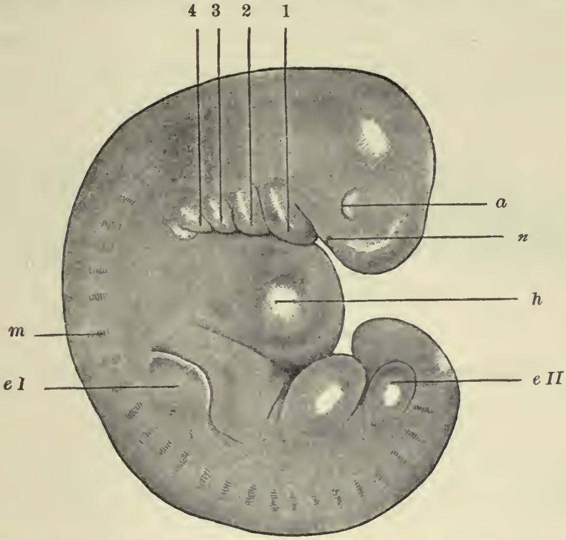


FIG. 3.—Human Embryo, about third or fourth week. 1–4, visceral arches with gill-slits between them: 1, mandibular arch; 2, hyoid arch; 3 and 4, first and second gill-arches. *a*, eye; *n*, nasal pit; *h*, cardiac region; *e I* and *e II*, fore and hind extremities; *m*, mesodermal somites.

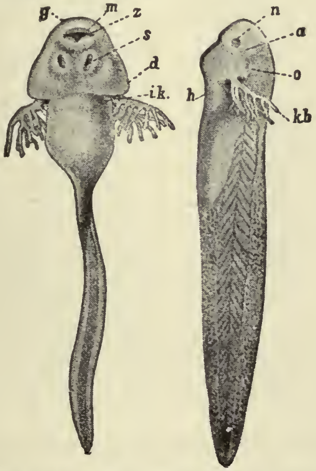


FIG. 4.—Tadpoles of *Rana temporaria*. *m*, mouth; *g*, upper jaw; *z*, lower jaw; *s*, sucking-disc; *kb*, external gills; *ik*, region of the internal gills; *n*, nose; *a*, eye; *o*, auditory vesicle; *h*, cardiac region; *d*, operculum.

resemblances to the lowest vertebrates, the fishes. Like these it has gill-slits, the same arrangement of the heart and of the arterial vessels, certain fundamental features in the development of the skeleton, etc. (2) Frogs in their tadpole stage have an organization similar to that which remains permanent in the case of certain Amphibia, the Perennibranchiata (fig. 5), which stand lower in the system; they have a swimming tail and tuft-like gills, which are lacking in the adult frog. (3) There are certain parasitic crustacea, which live upon the gills of fishes, and seem not at all like their relatives. They are shapeless masses which were formerly regarded as parasitic worms. Their systematic position was only determined by their embryology (fig. 6). Here it is

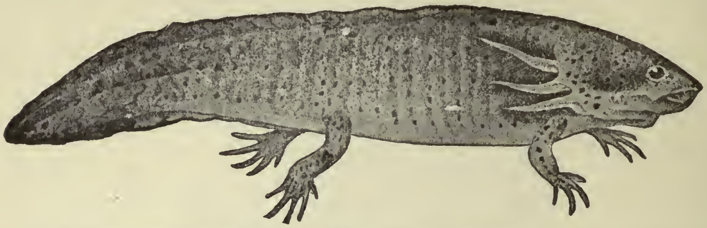


FIG. 5.—*Siredon pisciformis* (larva of *Amblystoma tigrinum*). (After Duméril and Bibron.)

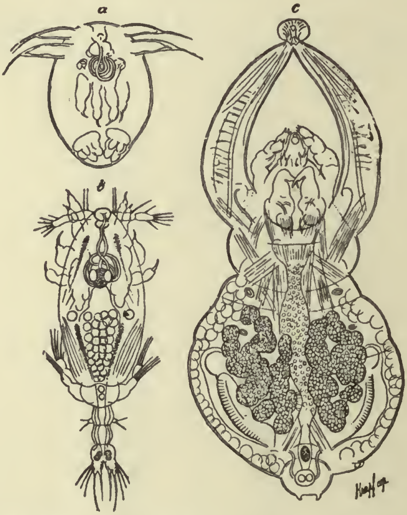


FIG. 6.—*Achtheres percarum.* *a*, nauplius-, *b*, cyclops-stage; *c*, adult female. (After Claus.)

shown that they pass through a nauplius-stage (fig. 6*a*), characteristic of most crustacea, and that they then assume the shape of small crustacea (fig. 6, *b*), like *Cyclops* (fig. 7, *A*), so widely distributed in fresh waters. Very often the males make a halt in the cyclops-stage while the female develops farther and assumes a shapeless form, so that there arises a very remarkable sexual dimorphism (fig. 8). All these examples, which can be multiplied by hundreds, can be explained in the same way. The higher forms

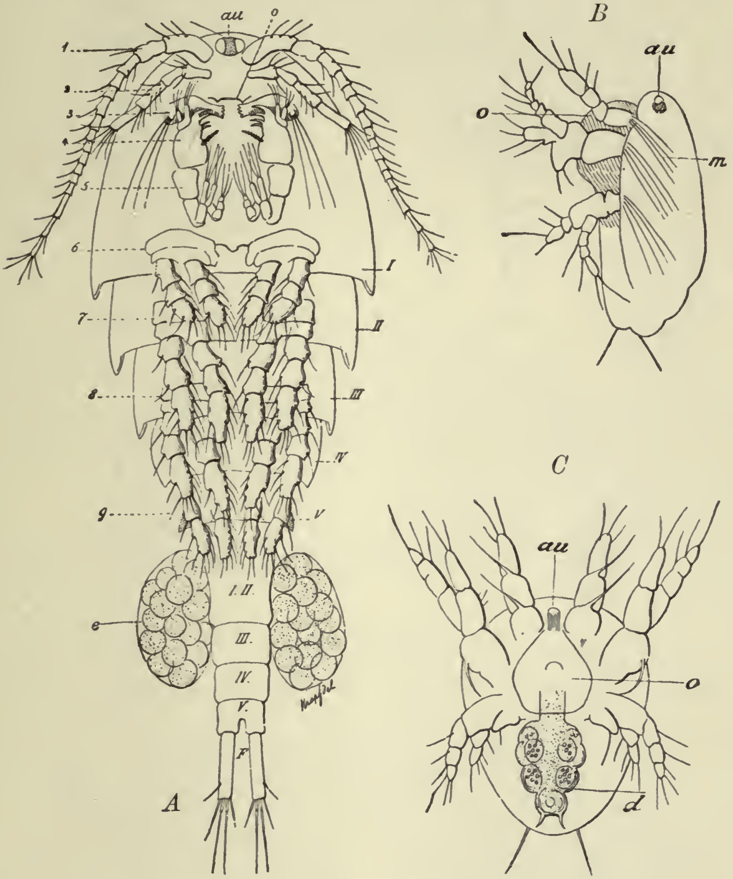


FIG. 7.—*Cyclops coronatus* (*A*) and also the nauplius in lateral (*B*) and in ventral view (*C*). *I*, head; *II–V*, the five thoracic, and behind these the five abdominal segments; *F*, furca; 1, the first, 2, the second, antennæ; 3, mandibles; 4, maxillæ; 5, maxillipeds; 6–9, the first four pairs of biramous feet, while the rudimentary fifth pair are hidden; *au*, eye; *o*, upper lip; *e*, egg-sacs; *d*, gut; *m*, muscle.

pass through the stage of organization of the lower, because they spring from ancestors which were more or less similar to the latter. Man in his embryological development passes through the fish stage, the frog the perennibranchiate stage, the parasitic crustacean first the nauplius- and then the cyclops-stage, because their ancestors were once fish-like, perennibranchiate-like, nauplius- and cyclops-like. Here is expressed a general phenomenon which Haeckel has stated in a general proposition under the name of ‘the Fundamental Law of Biogenesis.’ “The development history (ontogeny) of an individual animal briefly recapitulates the history of the race (phylogeny); i.e., the most important stages of organization which its ancestors have passed through appear again, even if somewhat modified, in the development of individual animals.”

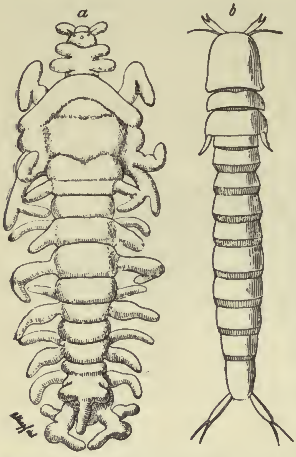


FIG. 8.—*Philicthys xiphiæ.* *a*, female (after Claus), × 4; *b*, male (after Bergsoe), × 13.

Examples of the Application of this Law.—*The Nervous System.*—This law applies as well to single organs as to entire animals. The central nervous system of the lower animals (echinoderms, cœlenterates, many worms) forms part of the skin; in its first appearance it belongs to the surface of the body, because it has to mediate the relations with the external world. In the case of higher animals, e.g., the vertebrates, the brain and spinal cord lie deeply embedded in the interior of the body; but in the embryo it is laid down likewise as a part of the skin (medullary plate) and which gradually through infolding and cutting off from this comes to lie internally. One can demonstrate this change of position by cross-sections through the dorsal region of embryos of different ages of any vertebrate (fig. 9).

The Skeletal System.—The skeleton of vertebrates is a further example. In the lowest chordates, amphioxus and the cyclostomes, the vertebræ are lacking, and in their place we find a cylindrical cord of tissue, the chorda dorsalis (notochord). In the fishes and Amphibia the notochord usually persists; but it is partially reduced and constricted by the vertebræ, which in the lower forms consist of cartilage, and in the higher of bone or a combination of bone and cartilage. Mature birds and mammals finally have a

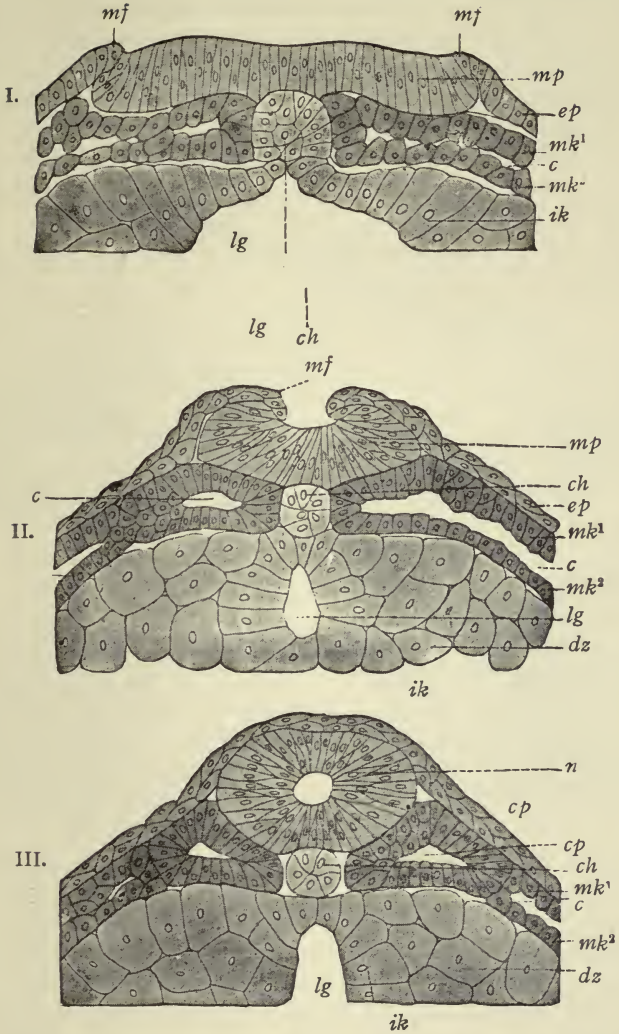

I.
mf
mf
mp
ep
mk1
c
mk-
ik
lg
lg
ch
mf
mp
c
ch
ep
II.
mk1
c
mk2
lg
dz
ik
n
cp
cp
III.
ch
mk'
c
mk2
dz
lg
ik

FIG. 9.—Cross-sections through the dorsal region of *Triton* embryos at different ages (from O. Hertwig). In *I* the medullary plate (anlage of spinal cord) *mp* is marked off from the skin (epidermis, *ep*) by the medullary folds (*mf*). In *II* the medullary plate by inrolling of the medullary folds is converted into a groove. In *III* the groove has closed into a tube (*n*), the spinal cord, which has separated from the rest of the ectoderm (epidermis). *C*, body cavity (cœlom); *ch*, notochord; *cp*, cavity of primitive somite (myotome); *dz*, yolk-cells; *ik*, entoderm; *lg*, lumen of gut; mk^1, mk^2, somatic and splanchnic layers of mesoderm.

completely ossified vertebral column; their embryos, on the other hand, have in the early stages only the notochord (amphioxus stage); later this notochord becomes constricted by the vertebræ (fish-amphibian stage) and finally entirely replaced; the vertebral column is in the beginning cartilaginous, only later becoming ossified. Comparative anatomy and embryology thus give the same developmental stage of the axial skeleton: (1) notochord, (2) notochord and vertebral column, the latter at first formed of cartilage, then of bone.

We have here spoken of a parallelism between the facts of comparative anatomy and those of embryology. But in reality we should expect a threefold parallelism; for according to the theory of evolution the systematic arrangement of animals is conditioned by a third factor—the historical development of the animal world, or phylogeny. The mile-stones of phylogenesis, the fossils, should give the same progressive series in the successive geological strata as the stages of forms found by comparative anatomy and embryology. We actually know instances of such threefold parallelisms. Comparative anatomy teaches that the lowest developed form of a fish's tail is the diphycercal (fig. 10, *A*); that from this the heterocercal (*B*), and from the heterocercal the homocercal form of tail-fin (*C*, *D*) can be derived. Embryologically the most highly developed fishes are first diphycercal, later heterocercal, and finally become homocercal. Last of all, paleontologically the oldest fishes are diphycercal or heterocercal, and only later do homocercal forms appear.

What has here been referred to is only a small fraction of the weighty proofs which morphology offers in favor of evolution; it can only serve to show how morphological observations can be employed. For the reflecting naturalist the facts of morphology are a single great inductive proof in favor of the theory of evolution.

Distribution of Animals.—From Animal Geography we learn that the present distribution of animals is the product of past hundreds and thousands of years. It will therefore be possible from this to figure out many of the earlier conditions of things, by proceeding with the utmost caution and overcoming extreme difficulties.

If we assume that from the beginning all animal species were constituted as they now are, they would then have been placed by the purposeful Creator in the regions best suited to their organization; their distribution would therefore have been determined by favorable or unfavorable conditions of life prevailing in the various regions, as the climate, food-supply, etc. If, on the other hand, we assume that the animal species have arisen from one another through variation, then there must have been, as an influence determining the manner of distribution, besides the conditions of existence, still a second factor, which we will call the geological. We know that the configuration of the earth's surface has changed in many respects in the course of the enormous space of time of the geological periods; that land areas, which earlier were united, have become separated by the encroachments of the sea; that by the upheaval of mountains important barriers to the distribution of animals were also formed. From the fact that

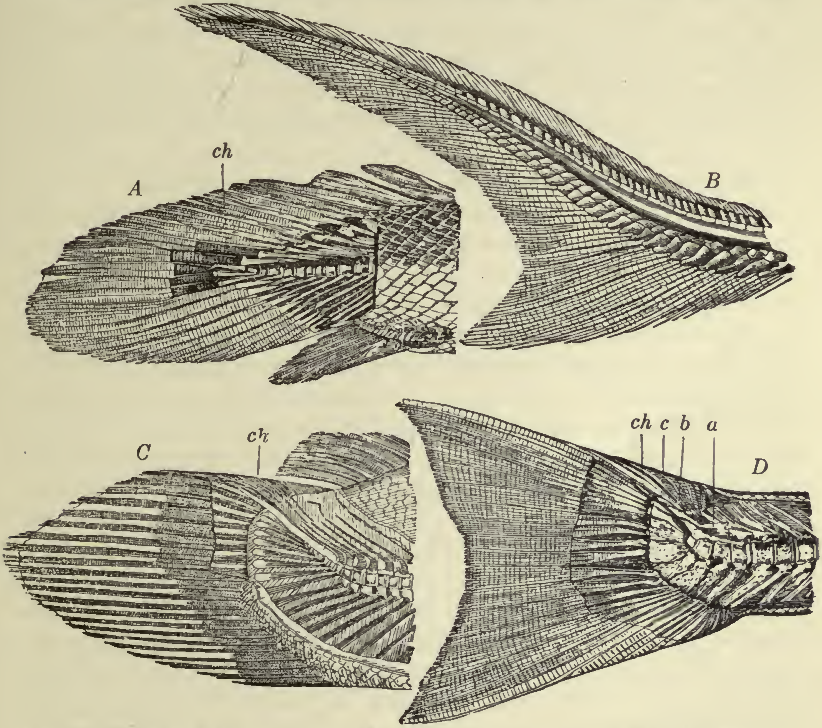


FIG. 10.—Tail-fins of various fishes. (From Zittel.) *A*, Diphycercal fin of *Polypterus bichir*. (Vertebral column and notochord divide the tail into symmetrical dorsal and ventral portions.) *B*, Heterocercal tail of the sturgeon. (As a result of an upward bending of the notochord and vertebral column the fin has become asymmetrical, the ventral portion much larger than the dorsal.) *C*, *D*, Homocercal fins, *C*, of *Amia calva*; *D*, of *Trutta salar*. (By a still greater upward bending of the notochord and vertebral column the dorsal portion has almost entirely disappeared and the ventral portion almost alone forms the fin, externally apparently symmetrical, but in its internal structure very asymmetrical.) *ch*, chorda; *a*, *b*, *c*, cover-plates.

these two changes—the changes in the earth's surface and in the animal world established upon it—have gone on hand in hand there follows necessarily the consequence that greater differences in the faunal character of two lands must result the longer they have developed independently of one another, without interchange of their animal populations, and the longer the inhabitants have been separated by impassable barriers. For the various groups the character of the barriers is different; terrestrial animals, which cannot fly, are hindered in their distribution by arms of the sea; marine forms by land barriers; for terrestrial molluscs high mountain ranges, which are dry and barren, or constantly snow-capped, are effectual.

Instances of Proofs.—Since attention has been called to these conditions, many geographical facts favorable to the theory of evolution have been ascertained: (1) Of the various continents Australia has faunally an independent character; when discovered it contained almost none of the higher (placental) mammals, except such as can fly (Chiroptera), or marine forms (Cetacea), or such as are easily transported by floating wood (small rodents), or such as could be introduced by man (dingo, the Australian dog); instead, it had remarkable birdlike animals (with beak and cloaca), and the marsupials, which have become extinct in the Old World and the opossums excepted, in America as well. The phenomenon is explained by the geological fact that in the earth's history Australia, with its surrounding islands, was certainly the earliest to lose its connexion with the other continents. While in the other four parts of the earth the higher vertebrates, which were developed from the marsupials and their lower contemporaries, came, by way of the lands connecting the various continents, to have a wide or even a cosmopolitan distribution, in isolated Australia this process of evolution did not go on, and its ancient faunal character was preserved. (2) As Wallace has shown, the Malay Archipelago is divided faunally into an eastern and a western half; within each group there are islands which, in spite of a different climate, have a very similar fauna. On the other hand, the faunal boundary ('Wallace's line') passes between the two islands Bali and Lombok, which have the same climate and geographically are very close together. But the depth of the strait in this region shows that here runs a boundary of extraordinarily long geological duration, and that in the earth's history Bali has developed in connexion with the western, Lombok with the eastern chain of islands. More recent studies make it probable that there is an island zone between the two in which a mixture of faunas occurs. Celebes especially belongs here. (3) A long time before Darwin, the renowned geologist Leopold von Buch, from the distribution of plants on the Canary Islands, had come to the conclusion of a change of species into new species; viz., on islands peculiar species develop in secluded valleys, because high mountain-chains isolate plants more effectually than do wide areas of water. M. Wagner has collected many instances which prove that localities inhabited by certain species of beetles and snails have been sharply divided by wide rivers or by mountain-chains, while in neighboring regions related so-called 'vicarious species' are found.

Causal Foundation of the Theory of Evolution.—The Darwinian theory, so far as the above exposition shows, is fundamentally like the theories of descent advocated at the beginning of this century by Lamarck and other zoologists; it is distinguished from these only by its much more extensive foundation of facts, and further in that it abandoned the successional arrangement overthrown by the type theory, and replaced it by the branched, tree-like mode of arrangement,—the genealogical tree. But still more important are those advances of Darwinism which relate to the causal foundation of the descent theory. The *doctrine of causes* which has brought about the change of species forms the nucleus of the Darwinian theory, by which it is especially distinguished from Lamarckism. In order to substantiate causally the change of species, Darwin proposed his highly important principle of 'Natural Selection by means of the Struggle for Existence.'

Artificial Selection.—In the development of this principle Darwin started from the limited and hence easily comprehended subject of Domestication, the artificial breeding of our races of domesticated animals. Many of these undoubtedly sprang from a single wild living species; others arose from several species, but now have the appearance of a single species. How have arisen such extraordinarily different races of pigeons—the fantail, the pouter, long- and short-billed pigeons, etc., the long- and short-horned cattle, the heavy, slow Percherons and the slenderly-built, fleet-footed Arabian horses? Undoubtedly through that same more or less conscious influence of man, which is still employed by the skilful animal-breeder. If he wish to obtain a particular form, he chooses from his stock suitable animals, which he pairs together if they in ever so slight a manner approach nearer than the others to the desired ideal. By repetition of this selection according to plan, the breeder attains a slow but sure approximation to the goal, since he uses for breeding only the suitable individuals from each new generation. If he wish, for example, to breed fantail pigeons, he selects from his stock animals with the most numerous and strongest tail-feathers. In the course of generations, then, characteristics cumulate; the number of pigeons having an increased number of tail-feathers becomes greater, and thus material is obtained which is adapted to a further increase in the number of feathers.

Factors of Evolution in Breeding.—The remarkable results of breeding which are well known to every observer of our domesticated animals depend mainly upon three factors: (1) *Variability;* the descendants of one pair of parents have the capability of developing new characteristics, thereby differing in appearance from their parents. (2) *Hereditability* of newly-acquired characters. This consists in the tendency of the daughter-generation to transmit the newly-developed characteristic to the succeeding generation. (3) *Artificial selection;* man selects for breeding purposes suitable individuals, and prevents a new character which has arisen through variation from disappearing through crossing again with animals of the opposite variational tendencies.

Factors of Evolution in Nature.—If we compare with the facts of domestication the conditions of animals living in the state of nature, we find again variability and heredity, as efficient forces, inherent in all organisms, though the former is not everywhere of the same intensity. There are many species which vary only slightly or not at all, and therefore have remained unchanged for thousands of years. But contrasted with these conservative species are in every group progressive species, active species, which are in the process of rapid change, and these alone are of importance in causing the appearance of new species. Since heredity is present in all organisms, there is only lacking a factor corresponding to artificial selection, and this Darwin discovered in the so-called 'natural selection.'

Natural Selection: Struggle for Existence.—Natural selection finds its basis in the enormous number of descendants which every animal produces. There are animals (e.g., most fishes) which produce many thousands of young in the course of their lives; not to mention parasites, whose eggs are numbered by millions. For the development of this animal throng there is no room on the earth; for even if we compute upon the basis of a slowly-multiplying animal, like the elephant, and assume that all the progeny live and reproduce normally, it would only be a few centuries before the entire earth would be occupied by herds of elephants. In order to preserve the equilibrium in nature great numbers of unfertilized and fertilized eggs, as well as young animals and many that are mature but have not yet attained their physiological destiny, must perish. Many individuals will undoubtedly be blotted out by purely accidental causes; yet on the whole those individuals which are best protected will best withstand adverse conditions. Slight superiority in structure will be of importance in this struggle for existence, and the possessors of this will gain an advantage over their companions of the same species, just as in domestication each character which is or is fancied to be useful to man insures advantage to the possessor. Among the numerous varieties that appear the fittest will survive, and in the course of many generations the fortunate variations will increase by summation, while destruction overtakes the unsuitable varieties. Thus will arise new forms, which owe their existence to 'natural selection in the struggle for existence.'

The 'Struggle for Existence.'—The expression 'struggle for existence' is figurative, for only in rare cases does an active conscious struggle decide the question of an animal's existence; for example, in the case of the beasts of prey, that one which by means of his bodily strength is best able to struggle with his competitors for his prey is best provided in times of limited food-supply. Much more common is the unconscious struggle: each man who attains a more favorable position by special intelligence and energy, limits to an equal degree the conditions of life for many of his fellow men, however much he may interest himself in humanity. The prey which by special craft or swiftness escapes the pursuer turns the enemy upon the less favored of its companions. It is noticeable that in severe epidemics certain men do not fall victims to the disease, because their organization better withstands infection. Here the term 'survival of the fittest,' which Spencer has adopted in preference to 'struggle for existence,' is better.

Instances of the Struggle for Existence.—Although the foregoing general considerations suffice to show that the struggle for existence plays a very prominent rôle in the organic world, yet on account of the importance of this feature it will be illustrated by a few concrete examples. The migratory rat (*Mus decumanus*), which swarmed out from Asia at the beginning of the eighteenth century, has since then almost completely exterminated the house-rat (*Mus rattus*) in Europe, and has made existence impossible for it in other parts of the world. Several European species of thistle have increased so enormously in the La Plata states that they have in places completely crowded out the native plants. Another European plant (*Hypochœris radicata*) has become a weed, overrunning everything in New Zealand. Certain races of men, like the Dravidian and Indian, die off to the same degree that other races of men, like the Caucasian, Mongolian, and Negro, spread. The more one attempts to explain that endlessly complicated web of the relations of animals to one another, the relations of animals to plants and to climatic conditions, as Darwin has done, so much the more does he learn to appreciate the methods and results of the struggle for existence. He will become conversant with many interesting phenomena, formerly unintelligible, which immediately find an explanation through this doctrine. Islands lying in the midst of the ocean have a disproportionately large number of species of wingless insects, because the flying forms are easily carried out to sea. For example, on the Kerguelen Islands, remarkably exposed to storms, the insects are wingless; among them one species of butterfly, several flies, and numerous beetles.

Sympathetic Coloration.—Very often, in regions which have a permanent or prevailing uniform color, the coat of the animals is distinguished by the same or at least by a similar hue; this phenomenon is called *sympathetic coloration.* Inhabitants of regions of snow are white, desert animals have the pale yellow color of the desert, animals which live at the surface of the sea are transparent; representatives of the most diverse animal branches show the same phenomenon. The advantages connected therewith scarcely need an explanation. Every animal may have occasion to conceal himself from his pursuers; or it may be his lot to approach his prey by stealth: he is much better adapted for this the closer he resembles his surroundings. Natural selection fixes every advantage in either of these directions, and in the course of many generations these advantages increase.

Mimicry is referable to the same principle, except that the imitation is not here limited to the color, but also influences form and marking. Frequently parts of plants are imitated, sometimes leaves, sometimes stems. Certain butterflies with the upper surfaces of the wings beautifully colored escape their pursuers by the rapidity of their flight; if they alight to rest, they are protected by their great similarity to the leaves of the plants around which they chiefly fly. When the wings are folded over the back, the dark coloring of the under sides comes into sight and the color on the upper side is concealed. The parts are so arranged that the whole takes on a leaf-like form, and certain markings heighten the imitation of the neuration of the leaf (fig. 11). Among the numerous species of leaf-butterflies there are different grades of completeness of mimicry; in many even the depredations of insects are imitated; in others the form and marking are still incompletely leaf-like, the marking being the first to come into existence. Among the grasshoppers also there are imitations of leaves, like the 'walking-leaf,' *Phyllium siccifolium*, *P. scythe*, while other nearly related forms more or less completely approach the appearance of dried, sometimes of thorny twigs (fig. 12, *a* and *b*).

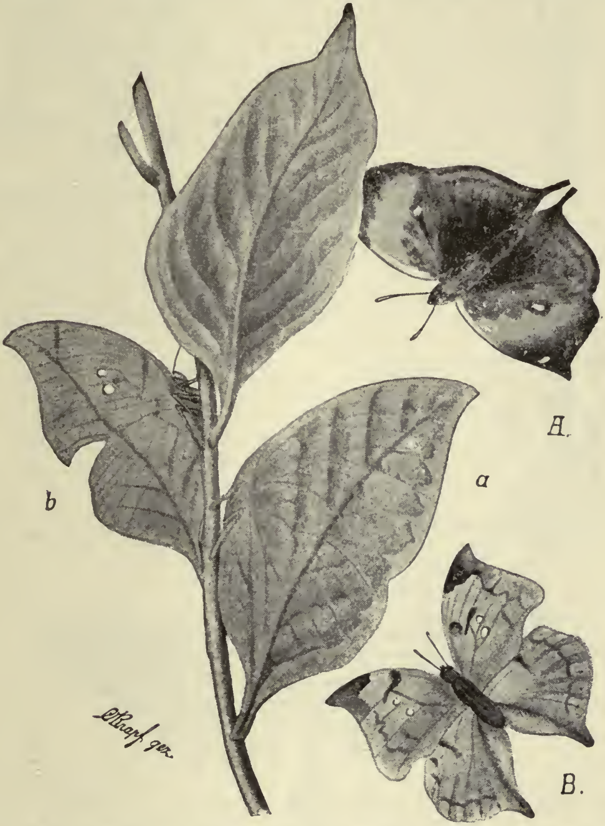


FIG. 11.—Leaf-butterflies. *A*, *Kallima paralecta*, flying; *a*, at rest. (After Wallace.) *B*, *Siderone strigosus*, flying; *b*, at rest. (After C. Sterne.)

Examples of Mimicry.—Very often insects are copied by other animals. Certain butterflies, *Heliconia*, fly in large swarms,

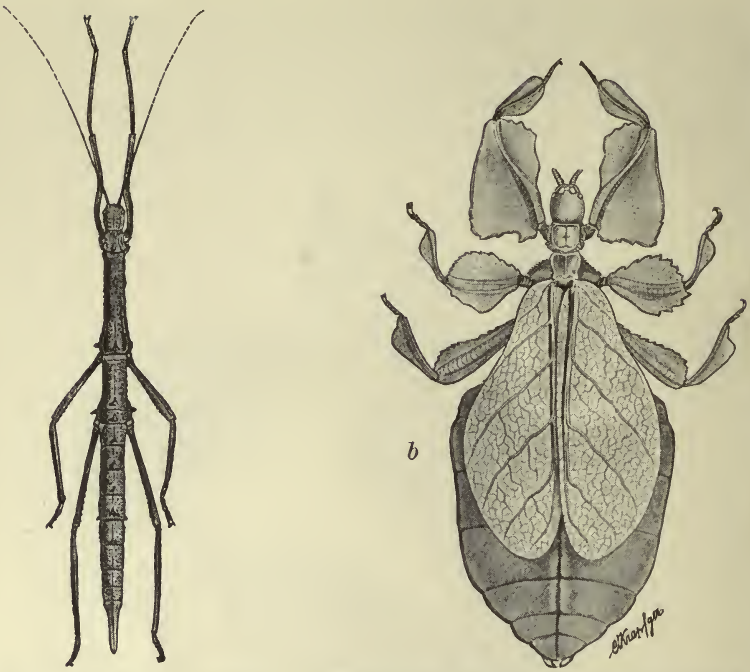


FIG. 12.—Grasshopper mimicry. *a*, *Acanthoderus wallacei* ♀. *b*, *Phyllium scythe* ♀.

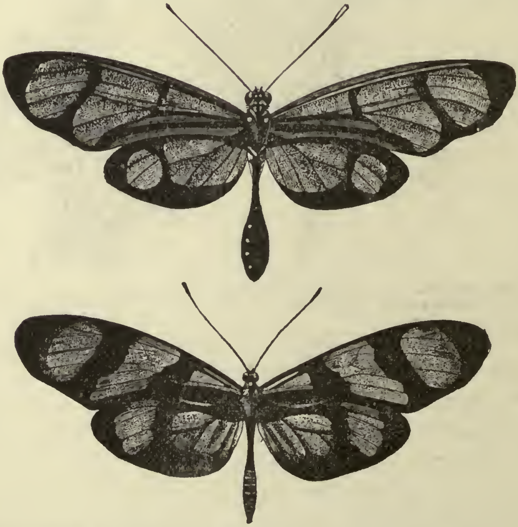


FIG. 13 —*Methona psidii*, a bad-tasting Heliconiid, copied by the Pierid, *Leptalis orise*. (After Wallace.)

clumsy and yet unmolested by birds, because they contain bad-tasting fat bodies. Another species of butterfly accompanies them (Pieridæ), which does not taste bad, and yet are not eaten, because in flight, in cut, and marking of the wings they imitate the *Heliconiæ* so closely that even a systematist might easily be confused (fig. 13). In a similar way bees and wasps, feared on account of their sting, are imitated by other insects. In Borneo there is a large black wasp, whose wings have a broad white spot near the tip (*Mygnimia aviculus*). Its imitator is a heteromerous beetle (*Coloborhombus fasciatipennis*), which, contrary to the habit of beetles, keeps its hinder wings extended, showing the white spot at their tips, while the wing-covers have become small oval scales (fig. 14).

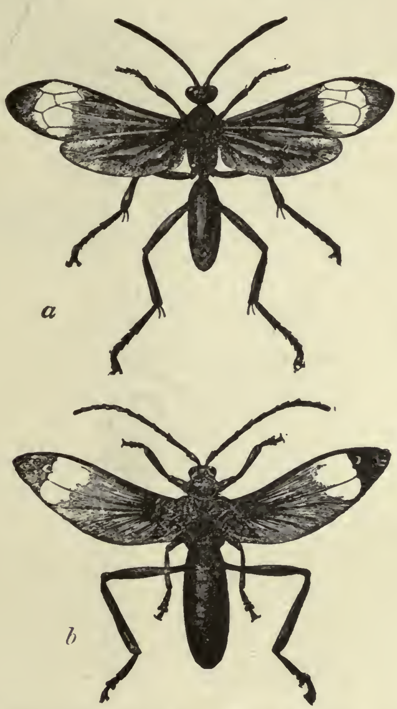


FIG. 14.—*a*, *Mygnimia aviculus*, a wasp imitated by a beetle; *b*, *Coloborhombus fasciatipennis*. (After Wallace.) ¾ nat. size.

Sexual Selection is a special phase of natural selection, chiefly observed in birds and hoofed animals. For the fulfilment of his sexual instincts the male seeks to drive his competitors from the field, either in battle or by impressing the female by his special excellences. With strong wings and with spurs the cock maintains possession of his flock, the stag by means of his antlers, the bull with his horns. The birds of paradise by means of beautiful coloring win the favor of the females, most singing-birds by means of song; many species of the fowl by peculiar love-dances. Since all these characters belong chiefly to the male, and since it is only exceptionally that they are inherited by the female (and even then are less pronounced), it is almost certain that in a great measure they have been acquired by the males through the struggle for the female. In the case of birds a second factor has undoubtedly co-operated to impress distinctly the often enormous difference between the feathers of the male and of the female—as

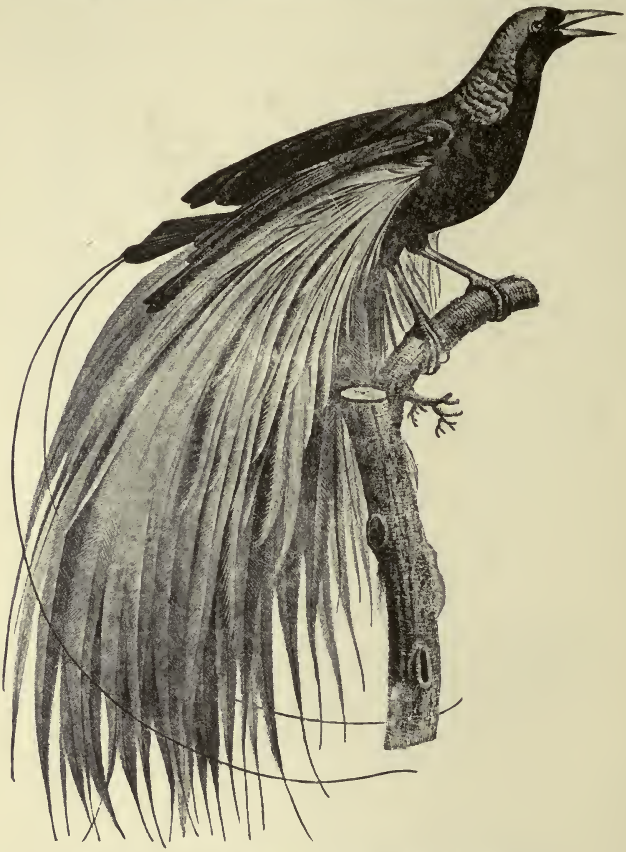


FIG. 15A.—*Paradisea apoda*, male. (After Levaillant.)

is shown, for example, in the case of the birds of paradise (fig. 15); for the nesting female inconspicuous colors and a close-lying coat of feathers are necessary in order that, undisturbed by enemies, she may devote herself to incubation.

On the Efficiency of Natural Selection.—In the course of the last decade there has been much controversy as to how far natural selection alone is a species-forming factor. A number of objectors dispute the possibility of fortuitous variations being utilized in the struggle for existence. It is not easy to see how many characters, especially such as are used in classification, can be of use to their owners. It can only be said that they have developed in correlation, that is in necessary organic connexion, with other important characters. But useful characters must be considerable in order to be seized upon by natural selection. Fortuitous variations with which Darwinism deals are too inconsiderable to be utilized by the organism and so to be of value in the struggle for existence. In most cases, too, alteration in one organ alone is not enough to be of value; usually a whole series of accessory structures must be modified. In short, there must exist a harmonious co-operation of parts, which presupposes a progressive and well-regulated development extending through a long space of time during which the struggle for existence could have exerted no directing influence. Thus, for example, the wing of a bird in order to be used for flight must have already reached a considerable size; the muscles for moving it, the supporting skeletal parts, the nerves running to it must have a definite formation and arrangement. Then there are difficulties in that most animals are bilaterally or

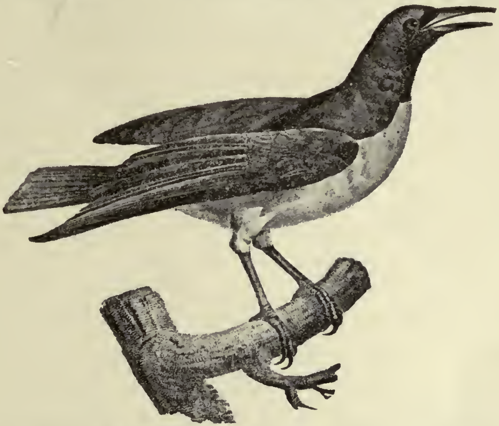


FIG. 15B.—*Paradisea apoda*, female. (After Levaillant.)

radially symmetrical, many in addition segmented. In all these cases the same organ is repeated two or more times. Organs which are repeated symmetrically and usually those which are segmental agree in general in structure. One must therefore admit that the alterations of chance must have occurred at at least two points simultaneously and in exactly the same way.

A further objection is that the action of natural selection would under ordinary conditions be negatived by unhindered crossing of the varying forms. If, for example, we do not isolate fantails from other pigeons, they will cross with these, and their descendants will soon resume the character of common pigeons. Finally, it has been claimed that for the formation of new species a simple variation of forms is not sufficient; it must reach still farther: (1) a variation in different directions, a divergent development of the individual members of a species; (2) the disappearance of the transitional forms which unite the divergent forms.

The objection that the struggle for existence cannot bring about the divergent development of individuals necessary for improvement is of least importance. It need only be added that of the many variations appearing at the same time in a species two or more may be equally useful; that then one set of individuals will seize upon one, another set upon the other advantage, and that in consequence of this both sets will develop in different directions. Consequently the intermediate forms which are not pronounced in the one or the other direction will be in an unfavorable position, and must carry on the struggle for existence with both groups of partially differentiated companions of their species, and, being less completely adapted, must fall.

More important are the first two objections; they have led to theories which originally seemed destined to complete the Darwinian theory, but in the course of discussion they have more and more raised the claim of entirely supplanting it. In the following paragraphs will be found an outline of these theories, but it is to be taken into consideration that, at the present time, we are still in the midst of the reform movement, and it cannot yet be said whether they will be able to stand beside the theory of the struggle for existence or will supplant it.

Migration Theory.—To explain how characters newly formed by variation become fixed, and do not disappear again through crossing with differently modified individuals, M. Wagner has proposed the Theory of Geographical Isolation, or the Migration Theory. New species may arise if a part of the individuals of one species should take to wandering, or should be transplanted, and thus come to a new place, in which crossing with the companions of their species who were left behind is not possible. The same might occur, if the region inhabited by a species should by geological changes be divided into two parts, between which interchange of forms would be no longer possible. The animals remaining under the old conditions would retain the original characteristics; the wanderers, on the other hand, would change into a new species. Direct observations support this theory. A litter of rabbits placed at the beginning of the fifteenth century on the island of Porto Santo has in the mean time increased enormously and the descendants have taken on the characteristics of a new species. The animals have become smaller and fiercer, have acquired a uniformly reddish color, and no longer pair with the European rabbit. A further proof in favor of the theory of geographical isolation is the peculiar faunal character of regions separated from adjacent lands by impassable barriers, broad rivers or straits, or high mountains (comp. p. 42); especially instructive in this regard is the peculiar faunal character of almost every island. The fauna of an island resembles in general the fauna of the mainland from which the island has become separated by geological changes; it usually has not only these but also so-called 'vicarious species,' i.e., species which in certain characteristics closely resemble the species of the mainland. Such vicarious species have plainly arisen from the fact that isolated groups of individuals, scattered over the islands, have taken on a development divergent from the form from which they started. With all due recognition of the migration theory, it will never be possible by it alone to explain the multiformity of the organic world. In addition, it must be assumed that formerly the earth's surface possessed an enormous capacity for change; but the more recent investigations make it probable that the distribution of land and water has not varied to the degree that was formerly believed. The experience of botanists, too, teaches that several varieties can arise in the same locality and become constant.

Lamarckism.—While the migration theory agrees with Darwinism in this, that the new characters appearing through variation are to be regarded as the products of chance, yet it is just this part of the theory which has been subjected to searching criticism. Many zoologists have again adopted the causal foundation of the descent theory proposed by Lamarck and believe that the cause of species formation is to be found in part in the immediate influence of changing environment, in part in the varying use and disuse of organs, brought about by alterations in the conditions of life. Both principles, they say, are sufficient, even without the help of the struggle for existence, to explain the phylogenesis of organisms.

Influence of Environment.—To what extent can the environment bring about a permanent change in the structure of plants and animals? To decide this is no simple problem, on account of the complexity of the factors entering into the question.

In cases where the food-supply is altered, organisms change in a very remarkable manner and within a short time; but these changes (Nägeli's 'Modifications through Nutrition') seem to have no permanence. Plants which, found in nature in poor soil, are transplanted into rich soil, or *vice versa,* soon acquire quite a different appearance, and preserve this through the following generations, so long as they remain in the rich soil; but the plant quickly returns to its former appearance when replaced in its previous surroundings.

In general, a change seems to be the more permanent the more slowly it has developed. In researches upon the influence of environment, we can, therefore, rely soonest upon results if we experiment with slowly-working factors, such as light and heat, dry or moist air, different intensities of gravitation, of stimuli, etc., which can be excluded from the environment of the organism.

Use and Disuse.—Regarding the efficiency of *use and disuse,* there is no doubt that the shape of an animal is influenced to a great extent by the manner in which the organs are used. The organs which are much used will become especially strong and *vice versa* those which are not used will become weak. The only question is whether these, in the strict sense of the word, newly-acquired characteristics are transmitted to the offspring, or whether the descendants, in order to attain to the same stage, must not repeat in the same way use and disuse. In the latter case the cumulation of characteristics, and with it the possibility that these may become permanent, is excluded. It is to be regretted that accurate results are still lacking on a point so well adapted for experimental treatment. At this time rudimentary organs strongly favor the Lamarckian principle; for we see that cave animals, which for many generations have lived in darkness, are blind, either having no eyes, or only vestiges of them, incapable of function. This seems to justify the view that this condition is attributable to lack of use, since it has brought about a functional and anatomical incapacity, which has increased from generation to generation. Now we must believe that what is true for disuse must express itself in the reverse sense in the case of use.

Nägeli's Principle of Progression.—In conclusion, there is still to be considered the change of species from internal causes, to which von Baer gave the poorly adapted because easily misleading term "Zielstrebigkeit" (the striving toward an ideal), and which Nägeli has termed the 'perfecting principle,' or the 'principle of progression.' It cannot, indeed, be denied that each species is compelled, by some peculiar internal cause, to develop into new forms, independently of the environment, and up to a certain degree, independently of the struggle for existence. In all animal branches we see the progress from lower to higher going on, very often in a quite similar way, in spite of the fact that the animals live under very different conditions of development. We see how the nervous system lying near the surface in the lower animals becomes in the higher animals concealed in the depths of the body; how the eye, at first a simple pigment-spot, becomes in worms, arthropods, molluscs, and vertebrates, provided with accessory apparatus, as lens, vitreous body, iris, choroid, etc. Here we see an energy for perfection which, since it occurs everywhere, must be independent of the individual conditions of life, and must have its special explanation in the character of the living substance.

It is by no means justifiable to call an assumption, as here expressed, teleological, and to reject it as unscientific; rather the organism seems to be just as mechanically conditioned as a billiard-ball, whose course is determined not only by contact with the cushions of the billiard-table, but also in a large measure by its indwelling force, imparted to it by the stroke of the cue. An organism, too, is a store of energy which must necessarily from itself develop more, but it is of more extraordinary complexity, and to an equal degree also is independent of the external world. A complete independence is naturally never present, and Nägeli has not so maintained. Along with it rather goes always an 'action' of the external world, a modifying influence which is carried on by the external conditions of existence, either directly or by the mediation of use and disuse.

This exposition of evolution has been given in a rather detailed way, because in the history of zoology it is undoubtedly the most important feature. No other theory in the course of the development of zoological investigation has gained such a hold, none has propounded so many new problems and opened so many new fields for research. There is no other zoological theory which compares with it in value as a working hypothesis. To the many objections which have been made that the theory is insufficiently grounded, it can only be replied that in the present state of our knowledge it is the only theory which agrees with our experiences and explains these in a simple way and on a scientific basis. In this sentence is given the merit of the theory, but at the same time also a limitation of its applicability. For on the one side the statement attributes the merit in the applicability of the system to the necessity of the human mind for simple explanations of the facts of natural science, and on the other hand it makes the degree of correctness dependent upon the state, whatever it may be, of our knowledge. On both sides no constant quantities are involved. Many investigators see no necessity of reconciling paleontology and our knowledge of plants and animals. To such, therefore, the Darwinian theory proves just as little as any opposing theory. Meanwhile thoughtful naturalists will keep in mind that our knowledge of nature is making considerable advances, and is visibly becoming wider and deeper. It is possible, even probable, that these advances will lead to many modifications of the theory. For instance, the theory of the causes which condition the formation of new species will undergo numerous changes. On the other hand, we can affirm with great certainty that the principle of descent, which first obtained credence through Darwinism, will be a *permanent landmark of zoological investigation.*

GENERAL MORPHOLOGY AND PHYSIOLOGY

General Zoology: Animal Morphology.—In the vital phenomena of animals a certain degree of similarity can be followed through the entire animal kingdom; the way in which animals are nourished and reproduce their kind, how they move, and how they gain experience, is essentially the same in great groups, and even widely separated forms show many agreements. Corresponding to this, the apparatus which is concerned with the above-mentioned functions, the organs of nutrition and reproduction, of motion and sensation in their grosser and finer structure, and in their ontogeny, must be similar to one another and show evidence of some fundamental characters which always or frequently recur. All this needs a general explanation before we can go into a description of the separate branches of animals. This explanation is the subject of general zoology, specially of general anatomy and embryology, or animal morphology.

Œcology or Biology.—If by means of anatomy and embryology we have learned the general character of the animal organism, we must yet farther study its relations to the environment. For this study of the conditions of animal life, œcology or biology, we have to consider the geographical range of animals, their distribution over the surface of the earth and in the different depths of the sea; further, the reciprocal relations of animals and plants, and of beast to beast, as these find special expression in colony-building, symbiosis, parasitism, etc.

General Anatomy.—In the case of General Anatomy, with which we shall begin, the fundamental proposition will be, *How is an organism formed from its constituent parts?* We shall thus in spirit follow the opposite course from that which anatomy actually takes, for this resolves the animal body into its elementary parts, its organs, tissues, and cells. Instead of analytical we will pursue synthetic anatomy.

The synthesis of an organism, of which by general anatomy we can only gain an idea, actually takes place in nature during the development of every animal. Embryologically every organism is at some time a simple element, a cell; this divides and gives rise to tissues; from the tissues are formed organs, and from the organs the regularly membered whole of the animal body is combined. If the general ontogeny proceeds synthetically, it then agrees in its manifestations with the processes which go on in nature and which are accessible to direct observation.

GENERAL ANATOMY.

The Morphological Units.—The expression 'constituent parts of the animal body' can be used in a double sense. We can speak of the chemical units, the chemical combinations, which form the tissues; these are the subject of animal chemistry, and may therefore be passed over here. But we may also speak of the constituent units (morphological units) of the animal body; these are the *cells.* These and their transformation into tissues, organs, and entire animals are for us of vastly greater importance.

I. THE MORPHOLOGICAL UNITS OF THE ANIMAL BODY.

The Cell.—The study of the morphological units of the organic body first found a firm foundation in the cell theory. Every scientific study of the anatomy of plants and animals must therefore take the cell as its starting-point.

History of the Cell Theory.—The conception of the cell of animals and plants has in the course of time undergone many changes, which must be known to some extent in order to understand completely the name and the conception. When, in the seventeenth century, Hooker, Marcello Malpighi, and Nehemia Grew introduced the term into vegetable anatomy, they meant small chambers surrounded by firm walls and filled with air or fluid contents. When, also, early in the nineteenth century, it was correctly recognized that the cell is the anatomical and physiological vegetable unit from which all the other parts of the plant are formed, and when the English botanist Brown discovered in the interior of the cell that small body previously overlooked, the kernel or *nucleus*, the old conception remained, and as such was accepted by Schleiden in his cell theory. Schleiden added as new a completely erroneous view of the origin of cells: that in a sort of matrix (the 'cytoblast') first a granule, the nuclear body, was formed, then around this granule a membrane, the nuclear membrane, arose by precipitation, and around the thus completed nucleus a larger membrane (the cell membrane) was deposited. Hence for the formation of the cell the nucleus would be of most importance.

The Schleiden-Schwann Cell Theory.—Since it is the nuclei which are most easily seen in the animal body, and even now are particularly useful in deciding questions concerning the presence of cells, it is readily understood how Schleiden's theory, which placed the nucleus so much in the foreground, should have led Schwann to apply the cell theory to the animal kingdom, and thus raise it to a principle of general application. We usually, therefore, speak of the Schleiden-Schwann cell theory.

As a result of this theory the walls, the cell membrane, were regarded as most important for the function of the cell; through the cell membrane diffusion-currents must pass between the surrounding medium and the contents of the cell; the character of the membrane and of the cell-sap must determine the condition of the diffusion-currents, and hence the functional character of the cell; the different appearance of tissues depends chiefly upon the fact that the cells, spherical in the beginning, change their form; in the case of fibrillar connective tissue, for example, they increase enormously in length and become fine fibrillæ. Since the life of an organism is nothing else than the co-operative work of all its cells, they flattered themselves that through the cell theory and the discovery, brought about by it, of the physical unity of the animal and vegetable body they had made an important advance in the great problem of the physical explanation of the phenomena of life. Cell genesis also seemed, according to the theory, to be just as satisfactorily explained on a mechanical basis as the formation of a crystal. In the 'cytoblast' the nuclear bodies, nuclear membrane, and cell membrane must be formed by deposition just as in the process of crystallization.

Reform Movements.—Since that time our conception of the nature of cells has completely changed. The cell does not, after the manner of a crystal, arise as a new formation in a matrix, but it presupposes the existence of a living mother-cell, from which it arises by division or budding. Just so also the cell is not a physical unit, but is itself an organism which shows to us all the enigmas of life, the physical basis of which our investigations must ever keep in view as a goal, though it be still indiscernibly distant. The membrane and cell-sap are of quite subordinate importance for the existence of the cell; rather the most important thing in it is the previously disregarded substance, for which von Mohl introduced the name protoplasm. According to the newer conception *the cell is practically a small mass of protoplasm, usually, probably always, provided with one or more nuclei.* This newer conception of the cell has developed so gradually, and has so slowly supplanted the Schleiden-Schwann view, that the old name has been retained, although it no longer at all fits the new conception. We have indeed become so thoroughly accustomed to the name that we no longer notice the contradiction of terms when we call a solid lump without a membrane a 'cell.'

Discovery of Protoplasm.—The reformation of the cell theory was begun by discoveries which were made in very different regions and only lately have been brought to a focus.

1. At about the beginning of the nineteenth century, Bonaventura Corti and Treviranus had seen that the chlorophyl bodies, which cause the green color of plants, in many species stream around in a lively manner in the interior of the cell, but Mohl was the first to find out that this motion

was not active, but rather that they are moved by a homogeneous substance in which they are embedded. This substance, which Mohl, in order to bring it into prominence, named *protoplasma*, became by other studies still more important. In the reproduction of the simplest algæ, it was found that the protoplasm, together with the chlorophyl bodies, collected itself into an oval mass, and that this body left the cell membrane and swam freely in the water. Since the cell-wall no longer showed signs of life, while on the other hand the protoplasmic body came to rest and formed a new plant, it was shown beyond doubt that this was the most important constituent part of the cell (comp. fig. 115).

2. In the study of animal tissues the importance of the peculiar cell-substance, the protoplasm, was still more plainly brought out. Here, in spite of the long-prevailing preconceived idea, unbiassed observation led to the discovery that most animal cells had no cell-membrane.

3. Very important, finally, was the study of the lowest organisms, the Protozoa. Dujardin sought by extremely careful observations to prove that these animals had no organs, but consisted of a uniform granular substance, the *sarcode*. The sarcode alone could produce all the vital phenomena, such as movement, sensation, assimilation, previously ascribed to many organs. Dujardin's theory was stoutly contested by Ehrenberg and his school, but finally attained general acceptance through the epoch-making work of Max Schultze and Haeckel.

Schultze's Protoplasm Theory.—On the basis of these three series of observations, Max Schultze finally established the reformation of the cell theory briefly sketched above, when by accurate study of the appearance and the vital phenomena, and by means of numerous experiments, he proved that the cell-substance of animals, the sarcode of Protozoa, and the protoplasm of plants are identical, and that to this substance, for which he retained the name protoplasm, all the vital phenomena of animals and plants are referable in the ultimate analysis. The second important modification concerns the changes of cells into tissues. These follow not so much through changes of form and modification of the cells into the tissue elements, as Schwann thought, but rather by means of chemical changes. By means of its formative potentiality the protoplasm gives rise to non-protoplasmic structural parts, as, for example, connective-tissue fibrils, muscle fibrils, nerve fibres, etc. These give the various tissues their specific character and perform their functions. The tissues also retain as the source of life and formation the unemployed remnants of cells, the connective-tissue corpuscles, muscle corpuscles, etc. We will now trace out farther these two fundamental ideas in Max Schultze's 'protoplasm theory,' and thereby briefly sketch the elements of the modern theory of tissues.

Nature of the Cell.—The size of the animal cell varies to a considerable degree; the smallest elements are the male sexual cells, the spermatozoa, whose bodies, particularly in case of the mammals, are even less than 0.003 mm.; the largest, on the other hand, with the exception of the giant plasmodia of some

Mycetozoa, are the egg cells. The yolk of the bird's egg, which alone forms the egg in the narrower sense, apart from its coverings, has for a time the morphological value of a cell, and in the case of the ostrich egg may reach a diameter of several inches. The form of the cell is likewise variable. Free cells, whose form is not determined by the environment, are usually spherical or oval in the resting condition, as the egg cell shows; united into tissues, the cells, on the contrary, may be pressed together into polygonal or prismatic bodies, or may send out spindle- or star-shaped branching processes.

Protoplasm.—So there is left to characterize the cell only the constitution of its substance: the cell is a mass of protoplasm with one or more nuclei. It is not known whether protoplasm is a definite chemical body, which from its constitution is capable of infinite variation, or whether it is a varying mixture of different chemical substances. So, also, we are by no means certain whether or not these substances (as one is inclined to believe) belong to those other enigmatical substances, the proteids. We can only say that the constitution of protoplasm must, with a certain degree of homogeneity, have a very extraordinary diversity. For if we see that from the egg of a dog there comes always and only a dog, and indeed an animal with all his individual peculiarities, that a sea-urchin's egg, placed under the most diverse conditions, produces always a sea-urchin, that a species of amœba always performs only the movements characteristic of that species, we must assume that the functioning constituent part of this cell, the protoplasm, has in each case its peculiarities. We are driven to the assumption of an almost unlimited diversity of protoplasm, even if we concede an important share in the prominent differences to the nucleus, of which we shall speak later.

General Properties of Protoplasm.—The similarity of protoplasm, still recognizable through all its variations, expresses itself in its appearance and in its vital phenomena. Under slight magnification, protoplasm appears as a faintly-gray substance, sometimes colored yellowish, reddish, etc., by pigments taken up by imbibition, in which numerous strongly-refracting granules are embedded. The vital characteristics of this substance are *movement, irritability*, power of *assimilation* and of *reproduction.*

By using higher powers a finer structure can be seen in the protoplasmic substance, the 'homogeneous protoplasm' of earlier writers. The nature of this is as yet in question: a fine-meshed framework (filar substance, spongioplasm, cell reticulum) the interstices of which are filled with other material (interfilar substance, enchylema, ground substance). The dispute lies especially around the question whether this framework is formed of threads and trabeculæ or whether the appearance is not formed by small chambers, bounded by fine partition-walls (foam structure of protoplasm).

Movement of Protoplasm.—Movement expresses itself first in changes of form of the whole body—amœboid movement—and secondly in the change of position of the small granules in the interior of the protoplasm—streaming of granules. Examples of amœboid movement (fig. 16) are chiefly the movements of many Protozoa, and of the colorless blood-cells (leucocytes) of multicellular animals; here the protoplasmic body sends out coarser and finer processes, which may be again withdrawn, serving for locomotion and hence called pseudopodia or false feet. The streaming of granules can be observed in the interior of the cell-body, as well as in the pseudopodia extending from this. The pseudopodia may even be so fine as to be at the limits of visibility with our strongest magnifications (fig. 17), yet in them it can still be observed that the granules wander hither and thither like people on a promenade, simultaneously centripetally and centrifugally, some with greater, others with less speed. And yet the granules are only passively moved by the protoplasm, for if we feed the creature with some pigment granules, like finely-pulverized carmine, these granules show the same remarkable streaming. Indeed nothing better illustrates the great complexity in the structure of protoplasm than these extremely complicated phenomena of motion in such narrow limits as pseudopodia in general.

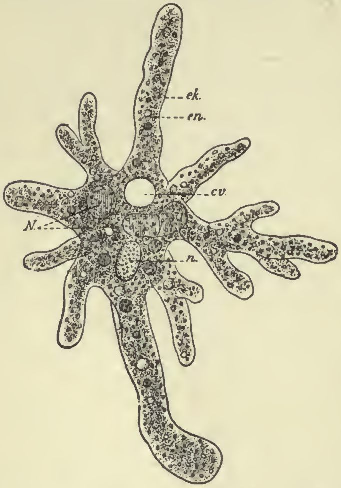


FIG. 16. — *Amœba proteus.* (After Leidy.) *ek*, ectosarc; *en*, entosarc; *cv*, contractile vacuole; *n*, nucleus; *N*, food-vacuoles.

Irritability of Protoplasm.—That amœboid movements and streaming of granules can be induced, brought to a standstill, and modified by mechanical, chemical, and thermal stimuli, is a sure proof of the irritability of protoplasm. Most important are the thermal stimuli; if the surrounding medium rise above the

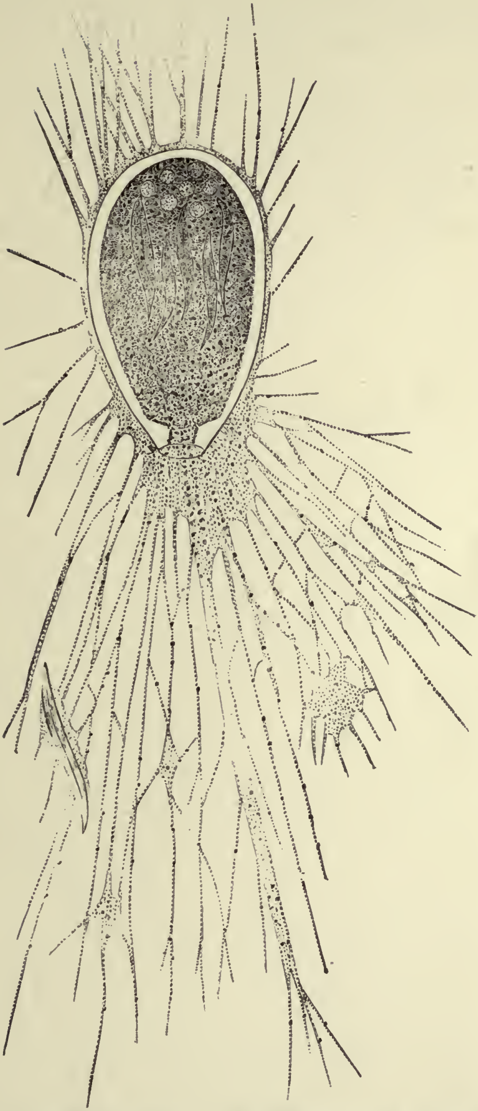


FIG. 17.—*Gromia oviformis.* (From Lang, after M. Schultze.)

ordinary temperature, the movements at first become more rapid up to a maximum: from that point begins a slowing, finally coming to a standstill.—*Heat-rigor.* If the high temperature continue much longer, or if it rise still higher, death results. The fatal temperature is found for most animals between 40° and 50° C. (104°–122° F.); its influence explains a part of the injurious effects which high-fever temperatures have upon the human organism. Like the heat-rigor, there is also a *cold-rigor,* induced by a sharp sinking of the temperature below the normal. This is accompanied by a gradual diminution of mobility; it results in death by freezing, which is, however, not so easily produced as death by heat. It is a remarkable fact that many animals, consequently their cells, may be frozen; and in this condition can endure still severer cold without dying. (For example: goldfish, a temperature of – 8° to –15° C.; frogs, to – 28°; newts, to – 25°).

Nutrition and Reproduction.—Irritability and power of motion are the prerequisites of assimilation, the change of food-substance into protoplasm. Most animal cells, for example almost all tissues cells, are not suitable for studying assimilation, because they live upon liquid nourishment. But certain cells of higher animals, the colorless blood-cells, and most unicellular animals can be fed also with solid substances; they take the food-particles into the midst of the protoplasm by flowing around them with the pseudopodia. They extract all the assimilable and reject the indigestible portions (fig. 16).

In the case of assimilation it is to be noted not only that the cells use the food which they have taken for their own growth and for replacing worn-out parts, but also that most of them have the power of producing substances other than protoplasm; for example, many Protozoa form organic shells or skeletons which are hardened with silica or lime. This formative power, the building of '*plasmic products,*' is, as we shall shortly see, the starting-point for tissue-formation.

Cell Nucleus.—The reproduction of protoplasmic bodies is synonymous with the division of the cell; but to understand this we must first consider the second important constituent, the *nucleus.* This is a body enclosed in the protoplasm, whose form, though definite for each kind of cell, shows in general wide variations. Usually it is a spherical or oval vesicle; but it may be elongated or club-shaped, bent into a horseshoe, with constrictions like a rosary, or even be branched, treelike (fig. 18); in many cells it is disproportionally large, so that the protoplasm surrounds it only with a thin layer, in others again it is so small that it can scarcely be found in the protoplasm among the other substances. Formerly, on this account, it was in very many cases overlooked, and even now it can often be demonstrated only by great care, and by employment of a special technique based upon the microchemical reaction of the nuclear substance.

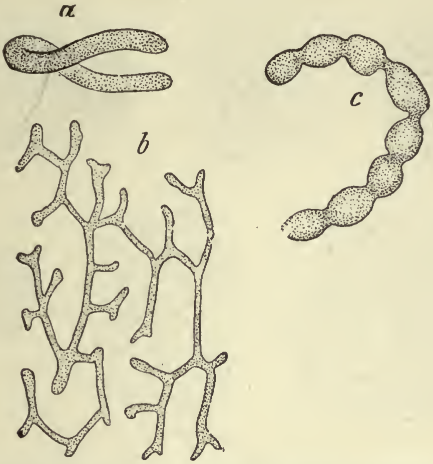


FIG. 18.—Various forms of nuclei. *a*, horseshoe-shaped nucleus of an Acinete; *b*, branching nucleus from the Malpighian vessel of a Sphingid larva; *c*, rosary-shaped nucleus of *Stentor cœruleus*.

The Nuclear Substance.—The nuclear substance is distinguished from protoplasm, among other ways, by its greater coagulability in certain acids, e.g., acetic and chromic, which therefore are often used for demonstrating the nucleus. If in a living cell the nucleus be invisible on account of the similarity of its refraction to that of the protoplasm, the addition of 2% acetic acid will often bring it into sharp contour.

Structure of the Nucleus.—In its minute structure the nucleus affords a wonderful variety of pictures varying according to the objects chosen, but which are not sufficiently understood to permit of a single description accepted by all. According to their reactions to stains two substances in particular are distinguished: chromatin or nuclein (fig. 19, *ch*), which is easily stained by certain staining-fluids (carmine, hæmatoxylon, saffranin), and the achromatin or linin, which stains not at all or only under special conditions.

The achromatin forms a network or reticulum (according to another view a honeycomb structure) filled with a nuclear fluid, bounded externally by a nuclear membrane, easily isolated in large nuclei. If little nuclear fluid be present, and the reticulum consequently be coarse-meshed, the nucleus seems compact. If the fluid be abundant, the nucleus appears vesicular. This is especially the case when the lines of the framework are separated by considerable amounts of nuclear fluid (fig. 19, *4*).

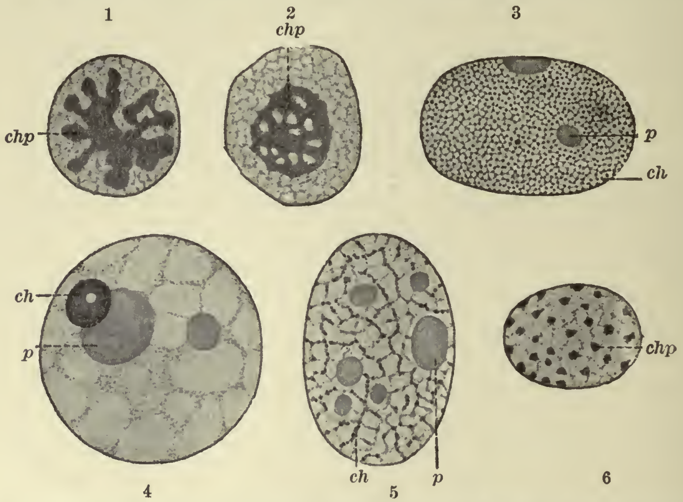


Fig. 19.—Vesicular nuclei with achromatic reticulum and different arrangements of the chromatin and nucleolar substance. *p*, plastin (nucleolar substance); *ch*, chromatin; *chp*, chromatin plus plastin 1 and 2, nuclei of *Actinosphærium*; 3, of *Ceratium hirundella* (after Lauterborn); 4, germinal vesicle of *Unio* (after Flemming); 5, nucleus with many chromatin nucleoli.

The chromatin enters into close relations with a less stainable substance, the plastin or paranuclein (also sharply distinct from achromatin). In the nuclei of Protozoa plastin and chromatin are usually intimately united, the first forming a substratum in which the latter is embedded (*chp*). The united substances are most frequently closely and regularly distributed as fine granules on the reticulum, so that the entire nucleus appears uniformly chromatic (fig. 18). More rarely the mixture collects into one or more special bodies, the chromatic nucleoli (*1*, *2*). The nucleolus is ordinarily a rounded body, more rarely branched (fig. 19, *1*).

In the nuclei of the Metazoa there may occur the same intimate mixture of plastin and chromatin (*6*). As a rule, however, the plastin (apparently not the whole, but a surplus) is separate from the chromatin. Thus there occur in the nuclei of many eggs nucleoli which contain, the one chromatin, the other exclusively plastin (*4*). In tissue cells only the plastin has the form of nucleoli (true or chromatin-free nucleoli, *5*), while the chromatin is distributed on the nuclear reticulum (chromatin reticulum). Somewhat the same may occur in the Protozoa (fig. 19, *3*).

Significance of the Cell Nucleus.—For a long time the functional significance of the nucleus in the cell was shrouded in complete darkness, so that it began to be regarded, in comparison with the protoplasm, as a thing of little importance. The evidence that the nucleus plays the most prominent rôle in fertilization has altered this conception. Then arose the view that the nucleus determines the character of the cell; that the potentiality of the protoplasm is influenced by the nucleus. If from the egg a definite kind of animal develop, if a cell in the animal's body assume a definite histological character, we are, at the present time, inclined to ascribe this to the nucleus. From this, then, it follows farther that *the nucleus is also the bearer of heredity;* for the transmission of the parental characteristics to the children (a fact shown to us by our daily experience) can only be accomplished through the sexual cells of the parents, the egg and sperm cells. Again, since the character of the sexual cells is determined by the nucleus, the transmission in its ultimate analysis is carried on by the nucleus. This idea has a further support in experiments on Protozoa. If one of these unicellular animals be cut into nucleate and anucleate halves, the latter sooner or later degenerates, the former persists and regenerates the lost parts. Within the nucleus it is probably the chromatin which controls the functions of the protoplasm and is accordingly (as observations on fertilization also seem to show) the bearer of heredity, while the achromatin is the seat of contractility, and as such plays a part in cell multiplication.

The Centrosome.—Besides the nucleus there frequently occurs a special body in the protoplasm, the centrosome, which on account of its small size and a behavior similar to achromatin with reference to staining-fluids was long overlooked, and even now its demonstration is difficult. It is apparently well distributed among the Metazoa, but is absent from most Protozoa. In many it appears only at certain times and then disappears. What is known of it makes it probable that it is a derivative of the nucleus, a part of the achromatin which has left the nucleus; in other cases possibly a second nucleus which by degeneration has lost the chromatin and retained only the active nuclear substance, the achromatin. In its function the centrosome is a specific organ of cell division which controls both the division of the nucleus and that of the cell itself.

Multiplication of Cells.—Increase in cells occurs exclusively by division or by budding (gemmation). Most common is binary division in which a circular furrow appears on the surface of the cell, deepens and cuts the cell into two equal parts. Multiple division is more rare and can only occur in multinucleate cells. Here the cell divides simultaneously into as many (sometimes hundreds) daughter-cells as there were nuclei present. In all forms of division the similarity of the products is characteristic, while in budding the resulting parts are unequal. In budding one or more smaller daughter-cells, the buds, are constricted from a large mother-cell (fig. 20).

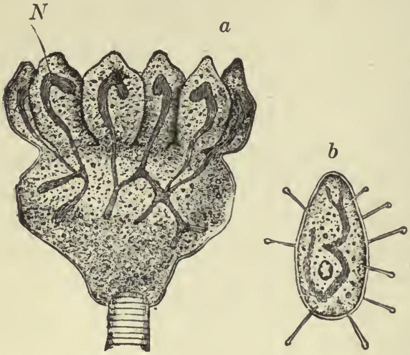


Fig. 20.—Cell budding. *Podophrya gemmipara* with buds (*a*) which separate and form free young (*b*). *N*, nucleus.

Direct Cell Division.—Every cell division is accompanied by nuclear division or at least presumes that nuclear division has previously occurred. Direct and indirect division are recognized. Direct division is most common in Protozoa, and especially in nuclei with abundant chromatin (fig. 20, 145). The nucleus is elongated and is divided by constriction, in the same way that the cell itself constricts. Since the protoplasm has no special arrangement with regard to the dividing nucleus (the latter besides protected by its membrane), we must conclude that the nucleus divides itself and is not passively divided. The dividing force resides in the achromatic framework, which correspondingly often exhibits a certain arrangement, a fibrous structure in the direction of the elongating nucleus.

Indirect Cell Division, Karyokinesis.—Indirect cell division, karyokinesis or mitosis, is most beautifully shown in cells, poor in chromatin, which possess a centrosome. The process is introduced by a division of the centrosome (fig. 21). The daughter centrosomes migrate to two opposite poles of the nucleus, which now loses its membrane and becomes the nuclear spindle. The characteristics of the spindle are that it is drawn out into points at two poles which are indicated by the position of the centrosomes, while from these poles fine threads, the spindle-fibres, run to the centre or equator of the nucleus. These fibres are in many cases certainly derived from the achromatic nuclear reticulum, while in others a greater or less part in their formation is taken by the protoplasm. A debated point is the relations of the fibres in the equatorial plane of the spindle. Do all the fibres extend from pole to pole? Do all of them end in the equatorial plane, so that the spindle consists of two cones of fibres separated at the equator? Or, lastly, are fibres of both kinds present in the same spindle? It would appear that differences exist in these respects in different objects.

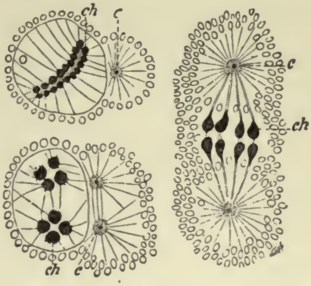


Fig. 21.—Spindle formation and division of the centrosomes in *Ascaris megalocephala*. (After Brauer.) *c*, centrosomes; *ch*, chromosomes.

All of the chromatin of the nucleus lies in the equator, united in the 'equatorial plate,' but by this must not be understood a connected mass but a layer of separate bodies, the chromosomes, for the chromatin of the nucleus divides early into particles which are rarely spherical or rodlike, but usually have the shape of U-shaped loops. These chromosomes are of equal size in the same cell, and, what is of greater theoretical significance, their number is identical in all the cells of all the tissues of one and the same species.

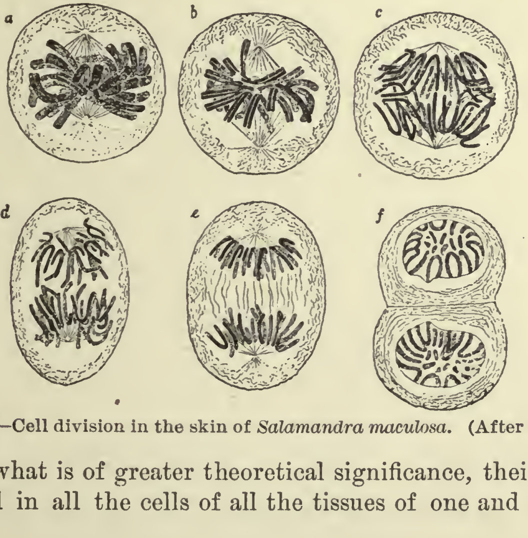


Fig. 22.—Cell division in the skin of *Salamandra maculosa*. (After Rabl.)

The first step in the karyokinetic formation of the daughter nuclei is the division of the chromosomes, which is usually completed in the equatorial plate (division of the equatorial plate), but occasionally may be completed at an earlier stage. The division is an accurate halving (fig. 22, *b*). The two halves of a mother-chromosome, the daughter chromosomes, now travel, under the influence of the spindle-fibres, towards the opposite poles of the spindle. In this way, by a splitting of the equatorial plate, the lateral plates arise, the elements of each uniting and producing the daughter nuclei. The centrosomes remain separate as division organs for the next nuclear division (fig. 22, *c*, *d*, *e*).

What further distinguishes the indirect from the direct cell division is the active participation of the protoplasm. The centrosome is the centre of a marked radiation of the protoplasmic reticulum (fig. 21). When the centrosome divides a double radiation (amphiaster) appears. Not only the spindle-fibres but the protoplasmic rays extend from the daughter chromosomes. Since the arrangement and degree of development of the protoplasmic radiations stand in certain relation to the phases of cell division we must recognize in them the expression of the effective forces (apparently contractile) in the protoplasm which cause cell division.

Between these two extreme cases of direct and indirect division are all possible transitions which show how the mechanism of nuclear division has been completed step by step, first, by the fibrous arrangement of the nuclear reticulum (spindle structure); second, through the development of the centrosome by which the division obtains an influence on the protoplasm; and third, by the development of the chromosomes. In reference to the latter the irregular division of the chromatin mass in direct division is relatively crude in comparison with the complicated processes involved in the formation and division of the chromosomes. These become intelligible if we regard the chromatin as the controller of the cellular processes and the bearer of heredity (*cf.* fertilization, *infra*). The more highly organized the animal, the more its cells have to inherit and the more important it is that the physical basis of heredity should be accurately divided in amount and in quality between the daughter cells. This is accomplished by mitosis.

Nuclear Fragmentation is to be distinguished from direct division; by it the nucleus becomes broken up into numerous parts which alone cannot live and as a rule degenerate. A typical example is afforded by the breaking up of the macronucleus during conjugation in the Infusoria (fig. 146).

Multinuclearity, Multicellularity.—Nuclear division and cell division commonly constitute a well-arranged mechanical process, the separate phases of which follow one another according to a definite law. The plane of division is perpendicular to the long axis uniting the two poles of the spindle. But the interrelation of cytoplasm and nucleus is by no means an unchangeable and indissoluble one, for very often nuclear division takes place without participation of the cytoplasm. If this process be repeated several times, there results a mass of protoplasm with many nuclei (fig. 23), which now on its part may become many cells, if subsequently the protoplasm divides according to the number of nuclei. Hence multinucleated protoplasmic masses are transitional stages between the simple mononucleated cell and a collection of several mononucleated cells, and in consequence of this are sometimes regarded as the equivalent of *one* cell, sometimes as equivalent to many cells, and are called sometimes multinucleated giant-cells, sometimes cell-complexes or *syncytia*. In the following pages a multinucleated mass of protoplasm will be considered as a single cell, because the essential feature of the cell is that it constitutes a vital unit, it has a physiological individuality, and in this respect a multinucleated mass of protoplasm behaves like a mononucleated; as the tissue cells and the Protozoa show, the plane of organization is not raised in the least by the multinuclearity. A change only begins at the moment when many particles of protoplasm are separated from one another, and many vital units are formed, i.e., when in place of multinuclearity a true multicellularity appears.

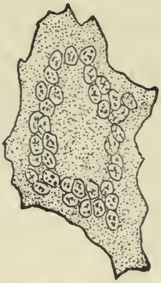


FIG. 23. — Giant-cell with many nuclei.

II. THE TISSUES OF THE ANIMAL BODY.

Definition of Tissue.—In the formation of tissues two processes are operative: (1) the multiplication of cells by means of division into cell-complexes, and (2) the histological differentiation of cells. A tissue, therefore, can be defined as *a complex of differentiated cells histologically similar.*

Nature of Histological Differentiation.—The histological differentiation consists chiefly in that the cells have definite form and definite position relative to the neighboring cells; in addition, there almost always occurs, as a second and more important feature, the histological modification of the cell. The fact has already been mentioned that the cell uses its food-material, not only for its own growth, for increase of its protoplasm, but also, in another manner, for forming substances, protoplasmic products, either in its interior (internal plasmic products), or more often on its surface (external plasmic products). *The histological change is the formation of specifically functioning plasmic products.* If we take as an example the manner in which a cell becomes a muscle fibre (fig. 24), we see that it continually secretes upon its surface new fibrillæ of specific muscle substance (in the case of the vertebrates, new cross-striated muscle fibrillæ), until finally the remnant of the formative cell, the muscle corpuscle, is contained in a mantle of muscle fibrillæ. In an analogous way, each tissue, upon histological examination, is seen to be composed of cells and plasmic products. The former control the formation, the renewal, and the sustenance of the tissue; the latter are the agents of its physiological function. The advantages of tissue formation are far-reaching, since in general they are connected with *division of labor* (frequently referred to later). So long as the cell unites in itself all the vital functions, these are incomplete because they mutually hinder each other in their free development; the plasmic product, on the other hand, has only the single function peculiar to it and can therefore discharge its duties with greater completeness. The muscle fibrillæ, the characteristic elements formed by the muscle cells, have preserved of the various properties of protoplasm only the capability of contraction; but this power of contraction is much more energetic and stronger than the mere movement of protoplasm. The nerve fibrillæ serve only for the transmission of stimuli, but in an extraordinarily more rapid and orderly manner than does simple protoplasm.

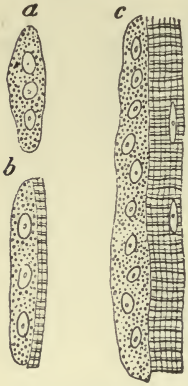


FIG. 24.—Formation of muscle fibrils in the frog. (Diagram.) *a*, formative cell; *b*, formative cell with two transversely striated muscle fibrils; *c*, formative cell with numerous muscle fibrils.

Classification of Tissues.—Since in every tissue its function interests us most, it would be natural to base the classification of tissues upon the function and the intimate structure connected therewith. For a long time the tissues have been arranged in four groups: 1. Epithelial tissue; 2. Supporting tissue; 3. Muscular tissue; 4. Nervous tissue. Within these, however, certain constituent parts of the animal body, to which indeed the term 'tissue' is scarcely applicable, find no shelter: these are the sexual cells, the blood, and the lymph. The former may be spoken of in connexion with the epithelium, the latter in connexion with the supporting substances.

1. Epithelial Tissues.

Morphology of Epithelial Tissues.—On several grounds the epithelia must be considered first. They are the oldest tissues; they are the first to appear in the animal kingdom, there being animals which consist only of epithelia. Further, each separate organism during the first stages of embryonic life consists only of epithelial layers, the germ-layers. With this is also connected the fact that in epithelial tissues the cells have undergone the least degree of histological change, and that the formation of plasmic products is subordinated.

Function of Epithelium.—The most important purpose of the epithelium is to form a protecting and excluding covering over surfaces, equally valuable whether the surfaces are external (surface of the body) or caused by cavities in the interior of the body (the body cavity, lumen of the gut and blood-vessels). The importance of the epithelia in this respect is shown by the fact that if the protecting layer be removed, inflammation arises and continues until the epithelium is regenerated. Only exceptionally do areas occur which are free from epithelium; the teeth of vertebrates, the antlers of stags, are parts of the body which, on account of their hardness, can exist, at least for a more or less considerable time, without epithelial covering.

Glandular and Sensory Epithelia.—By their superficial position epithelia are suited for presiding over two other functions: all substances which ought to be removed from the body—some because they have become useless, and consequently injurious (excreta), and others, as, for example, the digestive fluids, because they have to perform important functions (secreta)—must pass the surface, and are therefore separated by the epithelia; these are the *glandular epithelia*. Further, all influences of the external world chiefly impress the surface of the body, causing sensations; hence also certain epithelia are of the greatest importance for the reception of sensory stimuli, and serve for hearing, seeing, smelling, tasting, and touching. Such areas of epithelium are called *sensory epithelia*.

Covering Epithelium.—The covering epithelium consists of cells which, in order to serve the function of the tissue, are united by a small quantity of cementing substance. We speak of simple or of stratified epithelia, according as we find in sections running perpendicularly to the surface one or several superimposed layers (figs. 25, 26, 27).

Simple Epithelium. — Exclusively one-layered epithelia are found in all invertebrated animals and in Amphioxus; in the vertebrates, on the other hand, they are limited to the internal cavities of the body, and even here are occasionally, as always in the skin, replaced by a many-layered epithelium. According to the shape of the cells we distinguish cuboidal or pavement, flat, and columnar epithelium. In the case of pavement epithelium (fig. 25, *b*) the cells are all developed about equally in all directions of space, and because they have become compressed by lateral pressure have the appearance of cubical blocks or paving-stones. In columnar epithelium the long axis, the distance from the deeper to the peripheral end of the cell, is especially great (fig. 25, *c*); finally, in flat or squamous epithelium this is greatly

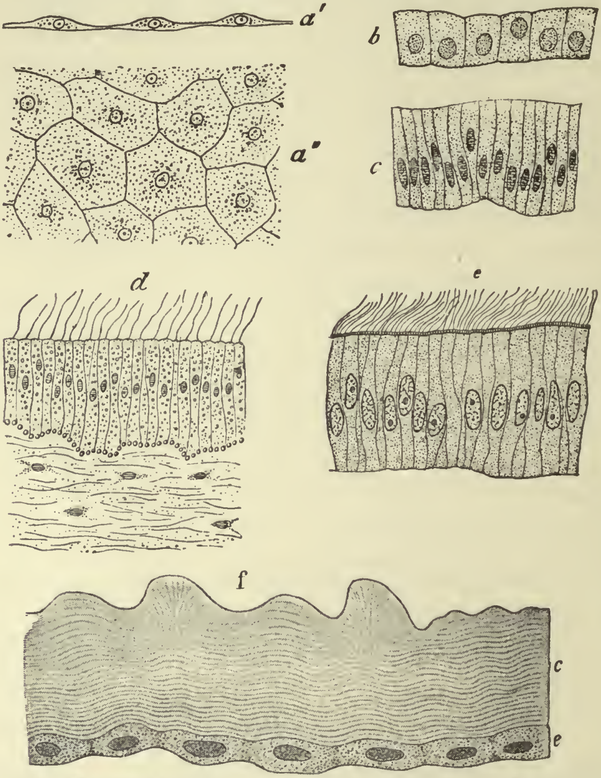


FIG. 25 — Various forms of epithelia. *a*, flattened epithelium of *Sycandra raphanus*, *a′* in cross-section, *a″* in surface view; *b* and *c*, cuboidal and columnar epithelium of a mollusc (*Haliotis tuberculata*); *d*, flagellated epithelium of an actinian (*Calliactis parasitica*); *e*, ciliated epithelium from the intestine of the fresh-water mussel; *f*, epithelium (*e*) with cuticle (*c*) of *Cimbex coronatus* (a wasp).

shortened (fig. 25, *a*) and the separate cells have become changed into thin plates.

Flagellated and Ciliated Epithelia.—Further differences which obtain in the three kinds of epithelium mentioned above are caused by the presence or absence of processes (cilia, or flagella) on the peripheral end of the cells. Both are fine threads which arise from the body of the cell, extend above the surface and here maintain an extremely lively motion. In case of flagellated epithelium (fig. 25, *d*) each cell has only *one* vibratile projection, but this is strongly developed; in the case of ciliated epithelium (fig. 24, *e*), on the other hand, the surface of the cell is covered with a thick forest of minute threads moving in unison.

Cuticle.—The majority of the one-layered epithelia are covered by a *cuticle,* a membrane which is secreted by the epithelial cells in general, and hence very frequently shows the impression of the cells as polygonal markings. In many cases thin and inconspicuous, it may in other instances become thickened into a very considerable layer, much thicker than the matrix layer of epithelium which secretes this cuticle. The cuticle is plainly composed of layers parallel with the surface, and forms a more effective protection for the surface of the body than does the epithelium; it becomes a protective armor, as shown, among other examples, by the calcareous shells of molluscs and the chitinous integument of insects (fig. 25, *f*).

Stratified Epithelia.—The protection furnished by the cuticle in the case of simple epithelium, may in the stratified be obtained immediately through a chemical change of a part of the cells themselves. In the stratified epithelia the cells of the various layers always can be distinguished by their form. The deepest layer consists of cylindrical cells; the superficial, on the other hand, of more or less flattened elements; between lie several layers of transitional forms, so that starting from the cylindrical cells we gradually pass through the cubical cells to the flat cells of the surface. As this arrangement shows, there exists a genetic connexion between the cell-layers: the lower cylindrical cells are in a state of active multiplication; their descendants, with gradual changes of form, become the superficial layers, here to replace an equal quantity of worn-out cells (fig. 26).

In the course of this change of position, the protoplasmic bodies may undergo an alteration; in the reptiles, birds, and mammals (fig. 27) they became cornified, first the margins, then the inner part of the cell, changing into horn. Of the living cell the nucleus remains for some time, until at length this vanishes, and then the cell becomes completely changed into a dead, horny scale. In the skin of the higher vertebrates the zones of the living protoplasmic, and the cornified cells no longer capable of life, are sharply marked off from one another. In cross-section they are readily distinguished as the stratum corneum (*sc*) and the stratum Malpighi (*sM*) of the skin (fig. 27). In the many-layered epithelia the cuticle has lost its importance, and it is either an inconspicuous boundary line or is entirely absent.

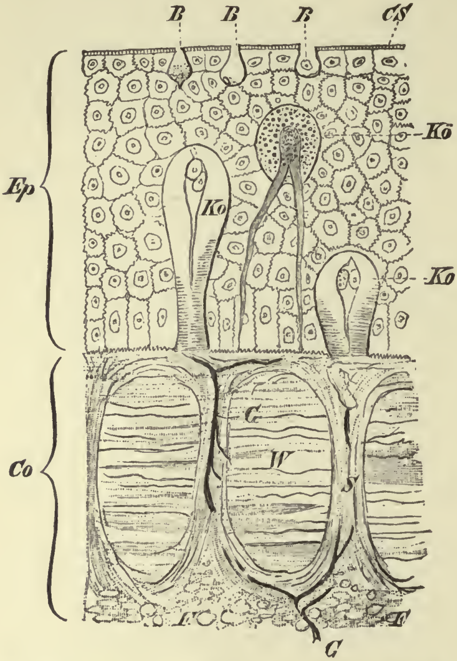


FIG. 26.—Section through the skin of *Petromyzon planeri*. *Ep*, the many-layered epithelium of the epidermis, including *B*, goblet cells; *Kö*, granular cells; *Ko*, *Co*, derma (with blood-vessels *G*), consisting of bundles of fibrils running horizontally (*W*) and vertically (*S*). (From Wiedersheim.)

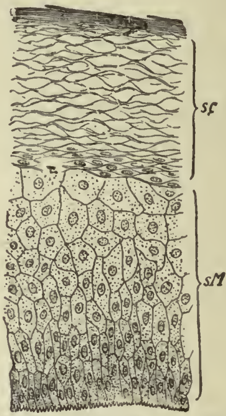


FIG. 27. – Stratified epithelium of man. *sM*, stratum Malpighi; *sc*, stratum corneum.

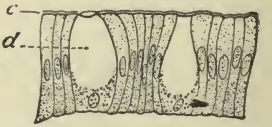


FIG. 28.—Single-layered epithelium of a snail. *c*, cuticle; *d*, goblet cells.

Glandular Epithelium.—Glandular epithelium is distinguished physiologically from ordinary pavement epithelium by the fact that it also produces secretions or excretions; anatomically it is recognizable by the presence of 'gland cells,' cells which carry on the secretion and, to a greater or less extent, reveal their character by their structure. Characteristic glandular cells are, for example, the goblet cells; here the secretion, usually mucus, is collected as a clear mass in the interior of the cell, the cytoplasm being compressed into a thin external wall, reminding one of a goblet containing the nucleus at its base (fig. 26, 28, *d*). Other gland cells are the granular cells, swollen bodies completely filled with secretory granules (fig. 26, *Kö*). Naturally all grades of transition between pavement and glandular epithelium occur. Commonly the latter name is only employed when the gland cells are especially numerous, thereby giving to the epithelial area a pre-eminently secretory character. This is especially the case with the structures which have the name of glands, among which we distinguish unicellular and multicellular glands.

Unicellular Glands.—Unicellular and multicellular glands increase the secretory surface by invagination. Invagination of a single cell produces the unicellular glands which are chiefly found among the invetebrate animals (fig. 29); a gland cell here becomes so enormous that there is no room for it in the epithelium, but it is pushed into the deeper, the subepithelial layers, the nucleated cell body, distended by secretion, sending up a slender process, the duct, to the epithelial surface.

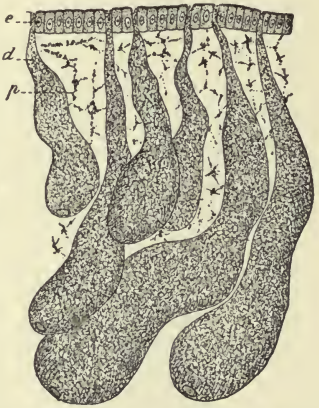


Fig. 29.—Unicellular glands from edge of the mantle of *Helix pomatia*. *e*, epithelium; *d*, unicellular glands; *p*, pigment cells.

Multicellular Glands.—In the formation of multicellular glands a considerable area of glandular epithelium grows as a cylindrical cord or tube from the surface down into the deeper tissues; this cord of cells seldom remains simple; it usually branches and forms the compound glands, which may consist of hundreds or thousands of glandular sacs, all emptying into a common duct. Among the multicellular glands are to be distinguished tubular and acinous (racemose) forms. In tubular glands (fig. 30) the simple or branched glandular pouches preserve the same tubular diameter from beginning to end; in the acinous glands (fig. 31), on the contrary, the blind end of the glandular pouch widens into a sac (acinus), largely composed of secretory cells, and related to the outer part of the glandular pouch, the duct, as grapes are to their stem. To the tubular glands belong the liver, kidney and sweat glands of man; to the acinous belong the salivary glands, not only of the vertebrates, but also of the arthropods and molluscs.

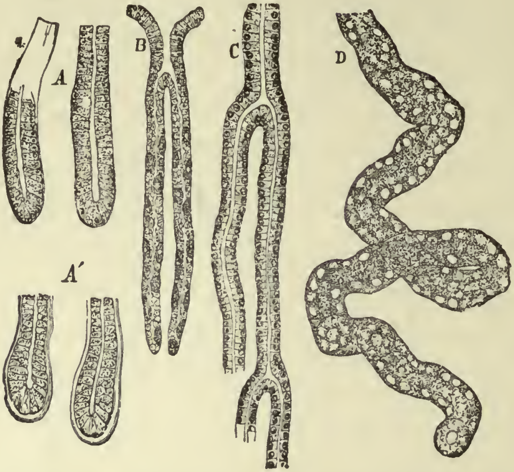


FIG. 30.—Tubular glands. (After Toldt.) *A*, glands of Lieberkühn from the human intestine; *A′*, of the conjunctiva of the eye; *B*, of the cat's stomach; *C*, from the medullary pyramids of the dog's kidney; *D*, from the cortex of the rabbit's kidney.

Sexual Epithelium.—The sexual cells may be considered in connexion with glandular epithelium. As the secretion of some

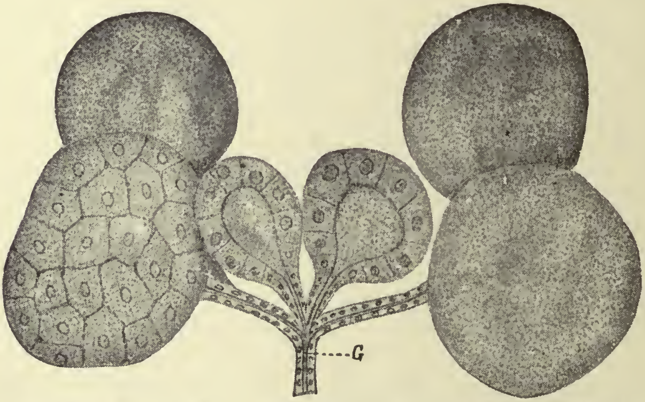


FIG. 31.—Acinous salivary gland of the aphid *Orthezia cataphracta*. (After List.) In some acini the nuclei and boundaries of the cells are shown.

glands must be expelled from the body, so the sexual cells are elements which differ from the rest of the organism, and must reach the exterior in order to perform their function. Just as the gland-cells are usually scattered among ordinary epithelial cells, so the sexual cells, almost without exception, lie embedded in epithelium; it may be in the epithelium of the skin (fig. 32), of the gut, of the body cavity, or of parts cut off from this (fig. 33). This connexion of the sexual cells with the epithelium has a deeper meaning in the fact that many organisms, and particularly organisms of low structure, consist exclusively of epithelia and therefore must necessarily develop their sexual products in epithelium. In other words, sexual and epithelial cells are the oldest elements of the animal body, and hence very early came into relation with one another.

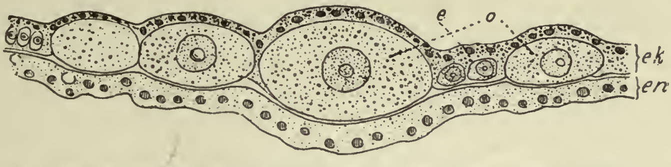


FIG. 32.—Germinal epithelium of a medusa. *ek*, ectoderm; *en*, entoderm; *o*, egg; *e*, epithelium.

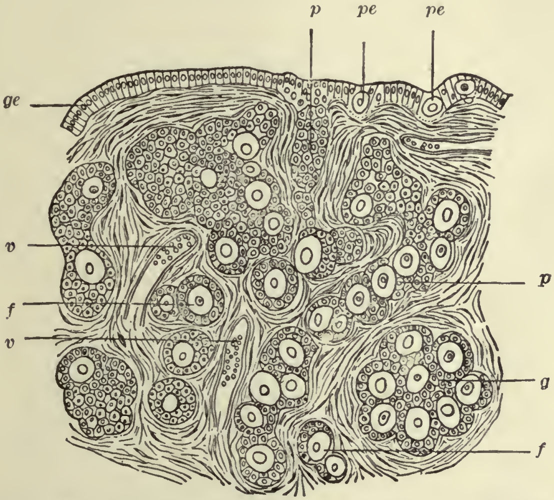


FIG. 33.—Section through the ovary of a new-born child. (After Waldeyer.) *ge*, germinal epithelium; *pe*, primitive egg in the germinal epithelium; *p*, egg-pouch; *g*, egg-nest constricted off from the pouchlike growth (*p*); *f*, single egg with follicle; *v*, blood-vessel.

Sexual epithelium (or, as it is often called, germinal epithelium) like glandular epithelium has a tendency to grow into the subepithelial tissues in the form of isolated or branching tubes (figs. 33, *p*, 34), and thus in many groups of animals the sexual organs bear the character of branched glands; for this reason one speaks as often of sexual glands as of sexual organs (fig. 34). The male and female cells, the specific elements of the germinal epithelia and of the sexual glands, differ in the fact that the eggs are generally the largest, the spermatozoa the smallest, cells of the animal body.

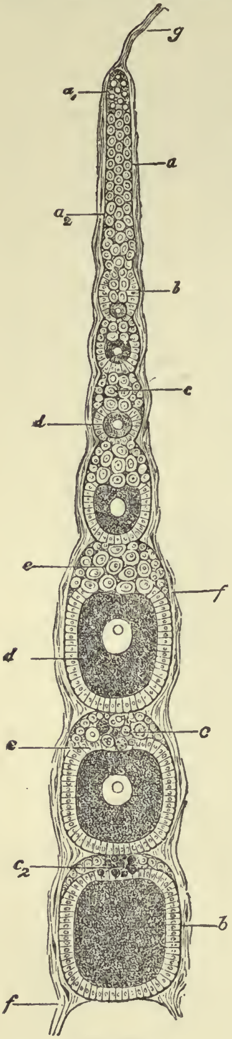


FIG. 34.

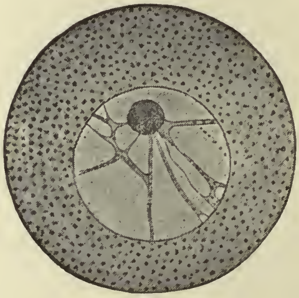


FIG. 35.

FIG. 34.—Ovarian tube of an insect, *Vanessa urticæ*. *a*, formative cell; *b*, follicular epithelium; *c*, nutritive cells; *d*, egg-cells; *f*, fibrous covering extending out into the terminal fibres (*g*). (After Waldeyer.)

FIG. 35.—Egg-cell of *Strongylocentrotus lividus*.

Egg-cell.—The *egg-cell* (fig. 35) as it is formed in the ovary varies in size according to the animal group: in case of the microscopic Gastrotricha it is less than 0.04 mm., in man about 0.2 mm., in the frog several millimetres, and in the large birds often several inches; however, only the yolk of the bird's egg is the egg-cell, the white of the egg and the shell are structures which are formed outside of the ovary in the oviduct. These remarkable differences in size are caused less by the quantity of the peculiar cell-substance, protoplasm (formative or primary yolk), than by the accumulation of deutoplasm (food or accessory yolk, also briefly called yolk). The function of the deutoplasm is to nourish the embryo during development, and hence consists of substances rich in fat and proteid, arranged in spherical oil-drops, or in fine granules or polygonal bodies, the yolk-granules. Its quantity, and therefore the size of the egg, is in part proportional to the length of time which the egg is cut off from any other supply of nourishment. In general we find the largest eggs in the case of the highly organized oviparous animals, where a long-continued course of development is necessary to lay the foundation of the manifold organs. Besides the protoplasm and deutoplasm, a cell nucleus or germinal vesicle (sometimes visible to the naked eye) surrounded by a membrane always occurs in the egg. Its contents are mainly the nuclear fluid, through which is distributed an achromatic network, and in addition the nucleolus, called also the *germinal spot.* Often there are multinucleolated germinal vesicles, especially in eggs which contain very much yolk.

The Spermatozoa, the morphological elements of the male reproductive product, are so small that their finer structure can be studied only with the strongest powers of the microscope (fig. 36, α and β). Easiest to recognize in them is the head, which from its variety of form—spherical, oval, sickle-shaped, etc.—often renders possible the specific determination of the spermatozoa. The head is the closely compacted chromatic part of the nucleus, and hence colors very deeply in staining fluids. Next comes an

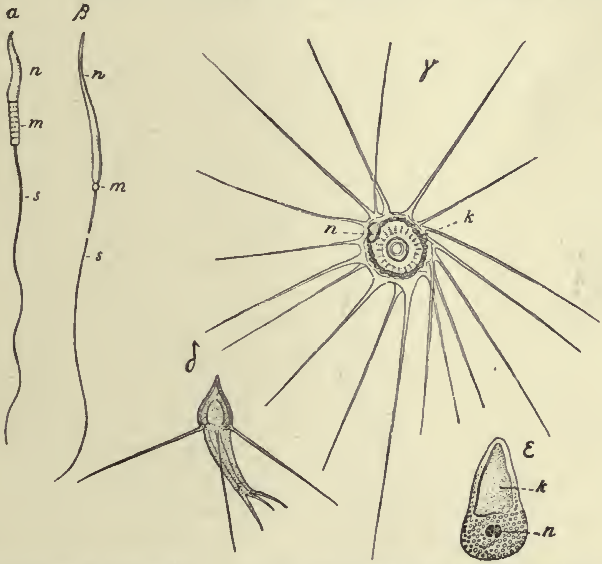


FIG. 36.—Various spermatozoa. *α*, of the night-hawk; *β*, of the green frog; *γ*, of the crayfish; *δ*, of a crab; *ε*, of the round worm (*Ascaris*). *n*, nucleus; *m*, middle piece; *s*, flagellum; *k*, homogeneous body.

unstaining second part, the middle piece, and then the tail, a long flagellum, which causes the active motility of the ripe spermatozoon. Cytoplasm is usually present only in an extremely thin layer surrounding the nucleus.

The spermatozoa of nearly all animals, except the nematodes and crustaceans, are constructed according to this type. In these two groups it is worthy of notice that the spermatozoa are remarkably large and incapable of motion, and that they enclose a homogeneous strongly refractive body (fig. 36, *k*), previously not found, the significance of which is not clear. The spermatozoon of *Ascaris* (fig. 36, *e*) has the form of a sugar-loaf with a broad rounded end, containing the nucleus; the spermatozoon of the crayfish (fig. 36, γ), on the other hand, has the shape of a cake-pan, from whose periphery springs a circle of fine, stiff, and pointed fibres.

The two kinds of spermatozoa found in a few animals are problematical. In the testis of one and the same individual of *Paludina vivipara* occur together hair-like spermatozoa with corkscrew heads and vermiform spermatozoa with a bunch of cilia on the hinder end. The first accomplish fertilization ; the physiological significance of the second is unknown.

The last modification of epithelium of which we have to speak is sensory epithelium, characterized by the connexion of certain of its cells, the sensory cells, with the finest twigs of branching nerves which arise in the central nervous system. This connexion may be of two kinds. In the first the cell (primary sense cell) is slender and filiform, the position of the nucleus being indicated by a swelling. The peripheral end is concerned with the reception of sensatory stimuli, while the deeper end is continued directly into the nerve ends and correspondingly is branched into two or more extremely fine processes which take on the character of nerve fibrillæ (fig. 37). In the second type the sensory nerve ends in a ganglion cell beneath the epithelium, which sends processes into the latter, the ends of these being applied to the sensory cell (secondary sense cell), the connexion being one of contact, not of

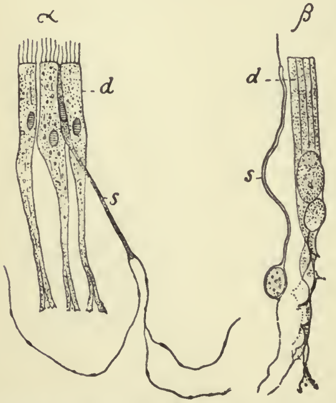


FIG. 37.—Sensory epithelium. *α*, of an Actinian; *β*, from the olfactory epithelium of man; *d*, supporting cells; *s*, sensory cells.

continuity. In both the peripheral end of the cell bears appendages for sense perception; auditory and tactile hairs, stronger processes in the case of olfactory and taste cells, conspicuous rods in visual cells. Almost without exception the sensory cells are part of the skin (ectoderm), or at least arise from it in development. This is true for sense organs like the eye and ear of vertebrates, which are separated from the skin by thick intermediate tissue, for in these the sensory epithelium (retina, crista acustica) is derived from the ectoderm.

Supporting Cells.—In the region of the sensory epithelium and between the sensory cells are found still other epithelial cells, which are not connected with nerves, but have accessory functions: they serve as supports for the sensory cells; in the eyes they contain pigment; in the auditory organs they often bear the otoliths, etc. They have the general name of supporting or sustentative cells.

2. Connective Tissues.

Contrast of Epithelium with Connective Tissue.—From a histological point of view there can be found no greater difference than exists between epithelium and connective tissue; the former belongs to the surface, the latter to the interior of the body; in the former the cells play the chief rôle, in the latter, on the contrary, their importance is subordinate to the plasmic products, the 'intercellular substances' which chiefly determine the character of the various kinds of connective tissue.

In spite of this contrast the connective tissues are genetically connected with epithelium. In embryos which at first consist only of epithelia the connexion can be directly seen. The epithelia secrete a gelatinous substance from their deeper surfaces into which separate cells migrate. Thus arises the embryonic connective tissue, the mesenchyme (fig. 107).

Function of Connective Tissue.—The primary function of connective tissue is to fill the spaces between the various organs in the interior of the body, thus connecting not only the single parts of the organs, but also the various organs themselves. In consequence of this the connective tissues contribute to the firmness of body, and are frequently employed in building up a skeleton. To accomplish this, substances which are usually firmer than protoplasm are formed on the surface of the cells, and, since they lie between the cells, these are called intercellular substances. In proportion as the intercellular substance increases in volume the cells themselves diminish and become inconspicuous corpuscles, the connective-tissue corpuscles, or, as seldom happens, entirely disappear. Since, in the connective tissues, the intercellular substances are most important, it is readily understood that the distinctions between the various kinds of connective tissue rest chiefly upon the differences of this intercellular substance. The following forms are to be distinguished: (1) cellular connective tissue; (2) homogeneous connective tissue; (3) fibrous connective tissue; (4) cartilage; (5) bone.

Cellular Connective Tissue shows the characteristics of the group least distinctly. It owes its name to the fact that the cells make up the chief mass, while the cell-products are inconsiderable. The cells are large and vesicular bodies which, like plant cells, are closely pressed together and are consequently polygonal (fig. 38). They have secreted between them a firm but thin layer of intercellular substance.

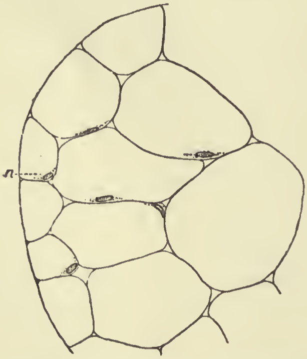


FIG. 38.—Cellular connective substance. Cross-section through the notochord of a newly hatched Trout.

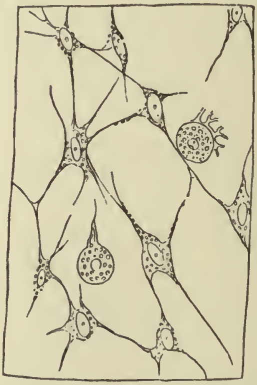


FIG. 39.—Homogeneous connective substance of *Sycandra raphanus*. (After F. E. Schulze.)

Homogeneous Connective Tissue.—In the case of *homogeneous connective substance* the intercellular substance (or matrix) is usually present in considerable quantity as a transparent mass, nearly invisible under the microscope, sometimes soft like jelly, often firmer (fig. 39). The gelatinous cells lying in it are either spherical or send branching processes into the matrix. Such processes may unite to form meshes which, like a pseudopodial network, unite cell to cell. Frequently the matrix contains, in addition, isolated firm fibres or threads, which, on account of their physical characteristics, are called elastic fibres, and consist of a substance (elastin) exceedingly resistant to all reagents. Finally, in the matrix there may develop the finer connective-tissue fibrils, the characteristic element of the next group; they may become so prominent by increase in number as to determine the character of the tissue.

Fibrous Connective Tissue is characterized by the rich supply of connective-tissue fibrillæ; these are fibres of extraordinary fineness, lying in a homogeneous basal substance, which is the less evident the richer it is in fibres. The fibres may be either confusedly arranged, crossing in all directions, or may run essentially parallel and in a definite direction. Between them are found the rounded, spindle-shaped or branched connective-tissue corpuscles (fig. 40). It is characteristic of vertebrates that the fibres are grouped into bundles. Each bundle is generally surrounded by connective-tissue corpuscles, metamorphosed into flat cells. The bundles, loosely interwoven, run in all direction (areolar connective tissue, 'cellular tissue' of the earlier authors) (fig. 41), or they may be almost parallel, forming a compact mass of fibres (tendinous tissue) (fig. 42). Since the fibrils of the fibrous connective tissue of the vertebrates have another peculiarity not met with elsewhere, in that they are composed of glutin, and upon boiling become gelatine or glue, it is well to reserve for these forms of tissue the special name connective tissue.

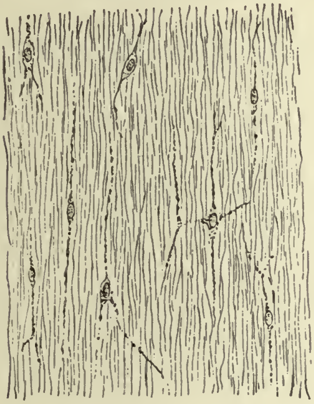


Fig. 40.—Fibrous connective tissue of an Actinian.

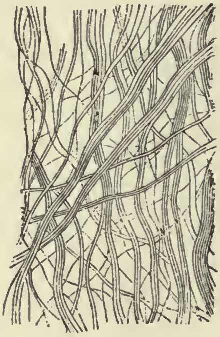


Fig. 41. — Areolar fibrous connective tissue. (After Gegenbaur.)

Elastic Tissue.—In all fibrous connective tissue there may appear, as a further constituent, elastic fibres; they may indeed supplant the ordinary connective-tissue fibrils and become the predominant element of the connective tissue, which is then spoken of as elastic tissue.

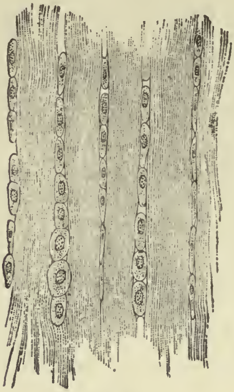


FIG. 42.

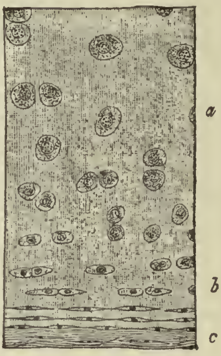


FIG. 43.

FIG. 42.—Tendinous tissue. (After Gegenbaur.)
FIG. 43.—Cartilage. (After Gegenbaur.) *c*, perichondrium; *b*, transition into typical cartilage (*a*).

Cartilage.—Cartilage and bone are likewise tissues which find their characteristic development only in the vertebrates. In its appearance cartilage is similar to the homogeneous connective substance of many invertebrated animals; the matrix is homogeneous and, at first glance, appears quite structureless (fig. 43), but, under the action of certain reagents, assumes a fibrous condition. This conduct, as well as the fact that the cartilage grows through changes of the perichondrium,—a thin, fibrillar skin covering its surface,—makes it more certainly evident that it is homogeneously fibrillar; and it is thereby distinguished from homogeneous connective substance since it is not, like the latter, a lower but a higher stage of tissue formation. It is worthy of note that the matrix of cartilage (chondrin) by cooking produces a kind of glue which differs from true or glutin glue in that it is precipitated by acetic acid. In the matrix the cartilage cells lie united in groups and nests, a mode of grouping pointing to their origin, since each group of cells has arisen from a single mother-cell by successive divisions. In cartilage also, elastic fibres are found; if present in great number, these change the bluish shiny, *hyaline cartilage* into the yellow-colored *elastic cartilage*.

Bone is the most complicated structure in the series of connective tissues. It consists of a matrix (ossein), closely allied to glutin, so intimately combined with inorganic constituents that it appears under the microscope as a homogeneous mass. The proportion of organic and inorganic substances varies according to the age and species of animal: in man, for example, there is 65% inorganic to 35% organic substance; in the turtle, 63% to 37%. Of the inorganic constituents, the most important is calcic phosphate, 84%; in smaller quantities, combinations of fluoric, chloric, carbonic acids and magnesia. Morphologically the matrix is composed of the bone lamellæ (fig. 44), whose arrangement is determined by the surfaces present in and upon the bone. In a hollow bone (like that of the upper arm or of the hand) there is an outer surface to which a fibrous skin, the bone-skin or *periosteum*, is closely applied; the presence of the marrow-cavity necessitates a second surface. Finally, the solid mass of the bone is permeated by the Haversian canals, which run chiefly in a longitudinal direction, united into a network by cross or oblique canals, and serve for the passage of blood-vessels. Since the bone lamellæ arrange themselves parallel to the surfaces mentioned, two systems may be distinguished in cross-section, the fundamental lamellæ and the Haversian lamellæ. The former are arranged parallel to the surface of the periosteum and of the marrow-cavity and form a mantle of concentric layers around the marrow-cavity. Into this groundwork the Haversian canals with their lamellæ enter, destroying and superseding the fundamental lamellæ coming in their way. The Haversian lamellæ are concentrically arranged around the lumen of the Haversian canals just as the fundamental lamellæ are around the marrow-cavity.

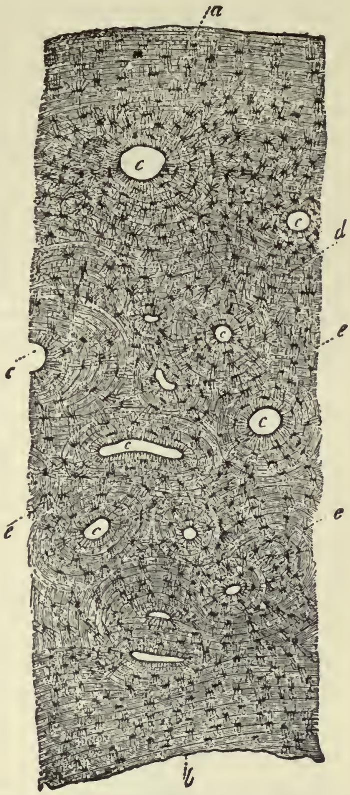


Fig. 44. — Cross-section through the human metacarpus. (After Frey.) *a*, surface of the periosteum; *b*, surface of the marrow-cavity; *c*, cross-sections of the Haversian canals and their system of lamellæ; *d*, fundamental lamellæ; *e*, bone-corpuscles.

Formation of Bone.—The stratification of bone is caused by its mode of origin. Where the bone borders upon the Haversian canals, the marrow-cavity, and the periosteum, there is transiently or permanently an epithelial-like layer of cells, *osteoblasts,* which secrete the bone-substance on their surface. Certain cells in the matrix participate in this secretion, and here give rise to the bone-corpuscles, which are distinguished from the cartilage-cells by their numerous processes ramifying through the matrix. The processes of a bone-corpuscle branch, and unite with the neighboring cells through fusion of the processes, an arrangement most beautifully seen in dried bone, because here the cavities and the canals of the matrix are filled with air. Special modification of bony tissue, the substance of fish-scales and of the teeth, called also ivory or dentine, should be mentioned.

Blood and Lymph, here treated in connexion with the connective substances, are in reality not tissues at all, but nutritive fluids. Two kinds of nutritive fluids occur in the vertebrates, red blood and the colorless, weakly opalescent, or cloudy white lymph. The blood of man and other vertebrates, consists of a fluid and the organized constituents. The fluid or *blood-plasma* is, apart from inorganic constituents, specially rich in proteids; after the removal of the blood from the blood-vessels a part of these separate by coagulation and form the blood-clot, made up of fibrin, leaving a fluid poor in proteids, the blood-serum. The organized constituents, the *blood-cells,* are distinguished as red and white blood-corpuscles. The latter, the *leucocytes,* are present in smaller numbers and have great similarity to the amœbæ found in water; they are particles of protoplasm, contain a nucleus, devour foreign bodies (for example, carmine granules injected into the blood), and move in the 'amœboid' manner by putting out pseudopodia (fig. 45).

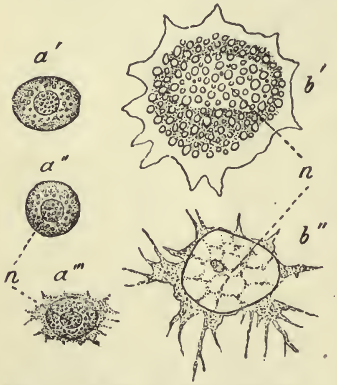


Fig. 45.—White blood-corpuscles. *a*, of man; *b*, of the crab (*n*, the nucleus).

Red Blood-corpuscles.—In the mature condition the red blood-corpuscles of vertebrates (fig. 46) are circular or oval discs, which by external influences (e.g., by pressure) may temporarily be bent, incised, or otherwise modified in form, but cannot actively change their shape, because they no longer consist of protoplasm. Embryologically they arise from true, nucleated, protoplasmic cells; whether these cells are identical with the leucocytes or are special 'erythroblasts' is still undertermined; but gradually the protoplasmic cell-body changes completely into a plasmic product, the stroma of the blood-corpuscle. If the nucleus be retained in this metamorphosis, there is a slight swelling in the centre of the disc; if, however, the nucleus degenerate, the bilateral convexity is replaced by a shallow concavity. In the latter case, one has, in reality, no right longer to speak of blood-cells, since all the characteristic constituents of the cell—nucleus and protoplasm—have disappeared. Systematically the red blood-corpuscles are of interest, since non-nucleate forms are found only in the mammals (fig. 46, *a*, *b*), nucleated ones in all the other vertebrates (*c*, *d*). The mammals also have circular, the other vertebrates oval, discs. To this, however, exceptions occur, since among the mammals the Typloda (camel, llama) have oval, the Cyclostomes have circular, blood-corpuscles.

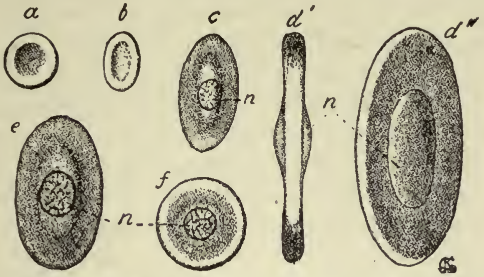


FIG. 46.—Red blood-corpuscles. *a*, of man; *b*, of the camel; *c*, of the adder; *d′*, of *Proteus* (seen from the edge); *d″*, surface view; *e*, of a ray; *f*, of *Petromyzon*; *n*, nucleus (all the blood-corpuscles are magnified 700 times, except *d*, which is magnified 350 times).

Hæmoglobin.—The red blood-corpuscles are the cause of the color of the blood, as well as the agents of one of its most important functions, the interchange of gases; both are connected with the fact that the stroma contains the coloring matter of the blood or *hæmoglobin*. Hæmoglobin belongs to the few crystallizable proteids and is remarkable for the presence of a small, though extremely important, quantity of iron, and also for its affinity for oxygen. Hæmoglobin containing oxygen, oxy-hæmoglobin, causes the carmine-like color of the so-called arterial blood; oxygen-free, 'reduced' hæmoglobin causes the dark red, faintly bluish color of venous blood.

Lymph is distinguished from blood by the entire lack of red blood-corpuscles and the slight coagulability of its plasma. Lymph is accordingly a proteid-containing fluid with leucocytes, which are here called *lymph-corpuscles.*

In the majority of invertebrated animals there is present only one kind of nutritive fluid, and not even this in every class; the fluid is called blood, although it is usually colorless. Where color is present, it is generally, if not always, a yellowish red or an intense red; this may, even as in the vertebrates, be caused by hæmoglobin (among the molluscs in *Planorbis, Arca tetragona, A. noæ, Solen legumen*, *Tellina planata*, *Pectunculus glycimeris,* and others; among the annelids in the Capitellidæ, *Glycera, Polycirrus, Lepræa,* leeches, and earthworms; among insects in *Chironomus*). Often other coloring matter occurs instead of hæmoglobin: in the cuttlefish, many snails, and in the lobster and Limulus, the oxygen is taken up by the bluish hæmocyanin, which contains a trace of copper; in the Sipunculids by hæmoerythrin, etc. The blood-plasma, as a rule, is the seat of the color (*Chironomus,* Hirudinea, earthworms, and most other annelids); only exceptionally do colored blood-corpuscles occur, as in the case of *Arca, Solen,* and the other mussels mentioned above, and also in the genus *Phoronis.* Colored elements containing hæmoglobin, identical with blood-corpuscles, are found besides in the cœlomic fluid of many annelids (Capitellidæ, *Glycera*, *Leprea, Polycirrus*), and in the ambulacral vessels of echinoderms (*Ophiactis virens,* some Holothurians). Most widely distributed in the invertebrate animals are the leucocytes, which are distinguished by their active amœboid movements; still even these may be absent, and then the blood is a fluid without any organized corpuscles.

3. Muscular Tissue.

Characteristics of Muscular Tissue.—Most sharply characterized functionally is the muscle-tissue, inasmuch as it is the agent of active movements in the animal body. Since active mobility occurs in protoplasm, it is important to notice the differences between the two kinds of movement. The distinctions lie in the direction and in the intensity of the movement. A mass of protoplasm has the capacity to move hither and thither in all directions, because in it there is a high degree of mobility between the smallest particles. Muscles and hence their separate elements, the muscle-fibres and muscle-fibrils, on the contrary, can shorten only by correspondingly increasing in diameter (fig. 47); they can therefore accomplish motion only in a definite direction, that of the axis of the muscle. The muscle-substance consequently is more limited in its movement than is protoplasm, but on the other hand it has the advantages of greater energy and greater rapidity. An observer conversant with the different kinds of motion is able to decide with considerable accuracy, from the intensity and rapidity, whether in a given case a movement has been brought about by the agency of protoplasm or by the contractile substance in the narrower sense (muscle-substance).

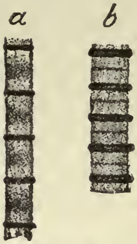


FIG. 47.—Transversely striated muscle-fibrils. (After Merkel.) *a*, in the resting, *b*, in the contracted state.

Formation of Muscle-substance.—These physiological considerations show that protoplasm and the contractile substance are morphologically different, and that therefore one must distinguish sharply between formative cells, or muscle-corpuscles, and the product of these cells, the contractile substance, just as in the case of connective tissue, between the connective-tissue corpuscles and the connective-tissue fibrils. This distinction actually occurs, but optically it is not equally demonstrable, for the reason that it is not prominent histologically. In animal histology there are recognized two kinds, it might even be said two stages, in the formation of muscle-substance, the homogeneous, or *smooth*, and the *cross-striated*. Since the former looks very similar to non-granular protoplasm, the boundary-line between it and the muscle-corpuscle is more difficult to recognize than in the case of the cross-striated muscle-substance, which in its minute structure is quite different in appearance from protoplasm. In cross-striated muscles the contractile portion consists of two substances regularly alternating with one another in the direction of the contraction of the muscle, of which the one is doubly, the other singly, refractive (figs. 24, 47, 50).

Smooth and Cross-striated Muscle-fibres.—The smooth muscle-substance represents a lower stage of development than the cross-striated, since it chiefly occurs in the less highly organized and more inactive animals. Interesting in this respect is the fact that in the two stages of development of one and the same animal the simple and inert polyp has smooth muscles, while the more highly organized and actively motile medusa has cross-striated muscles (fig. 48). The difference in their action has led in the vertebrates to a peculiar distribution of the muscle-substance, the smooth musculature being chiefly distributed to the internal organs, which are not under control of the will (involuntary muscles), while the musculature of the body, subject to the will and hence demanding more rapid action, is cross-striated (voluntary muscles). We must not conclude that the difference between smooth and cross-striated musculature coincides with the distinction between visceral and body musculature; it should be noticed that the body musculature of all molluscs is smooth, the visceral as well as the body muscles of many insects and crustacea, and the muscles of the heart of vertebrates are cross-striated.

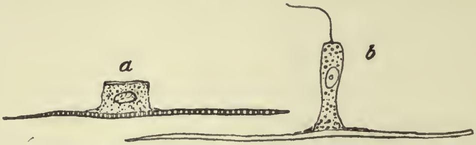


Fig. 48.—Epithelial muscle-cells. *a*, of a medusa; *b*, of an actinian.

It was pointed out above, in connexion with epithelia and connective tissue, that these tissues differed fundamentally. This contrast has its bearing in dealing with the muscles, for both epithelial and mesenchymatous cells may form contractile substances and therefore there are two genetically different kinds of muscles, the epithelial and the mesenchymatous (contractile fibre-cell). Both kinds of muscle-cells can *a priori* form smooth as well as cross-striated muscle-substance; but the collection of connective (mesenchymatous) tissue around inner organs has caused most contractile fibre-cells to be smooth, while most of the epithelial muscle-cells are cross-striated.

Epithelial muscle-cells are cells of which one end extends to the surface of the body or the surface of an internal cavity (body cavity, lumen of the gut, etc.), and may here have a cuticle, cilia, or flagella, while at the opposite end it has secreted contractile substance in the form of muscle-fibrils (fig. 48). They combine the double function of epithelial and muscle cells.

Contractile fibre-cells, on the other hand, are connective-tissue cells, which usually have surrounded themselves with a layer of contractile substance; corresponding to their origin, they have the form of connective-tissue cells, and are spindle-formed or branched; the branches arising from the ends of the cells (fig. 49). The similarity of form renders the distinction between ordinary connective-tissue cells and fibre-cells difficult; if the contractile layer on the surface be slightly developed, the distinction is impossible. To recognize the character of the elements, therefore, we must choose well-defined examples, in which the uninucleated or the multinucleated mass, the 'axial substance,' is sharply marked off from the muscle-mass, the 'cortical layer' (fig. 49, *c*, *d*, *e*).

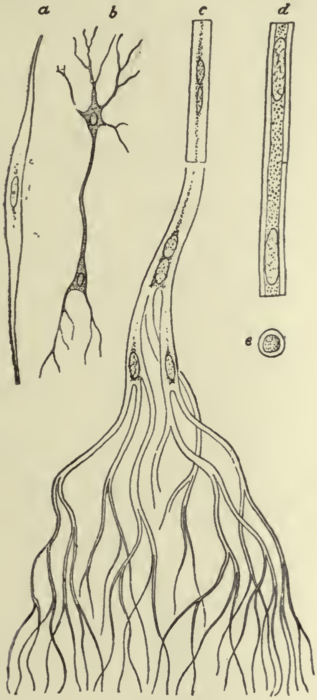


FIG. 49.

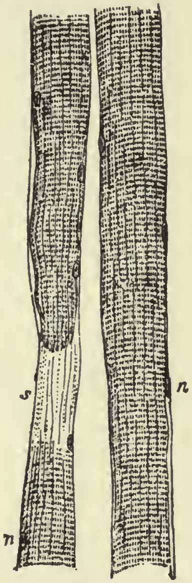


FIG. 50.

FIG. 49.—Contractile fibre-cells. *a*, of man; *b–e*, of Beroë (a Ctenophore); *b*, young fibres; *c*, branched ends; *d*, middle portion of a fibre; *e*, cross-section.

FIG. 50.—Cross-striated primary bundle. (After Gegenbaur.) *n*, nuclei; *s*, a point where the sarcolemma is plainly shown on account of the tearing of the fibres.

In vertebrates and arthropods the contractile fibre-cells occur in the vegetative organs as elements of the 'organic musculature'; on the other hand we find here the epithelial musculature in the cross-striated primary bundles, separated from the epithelium, and only developmentally referable to the epithelium of the body cavity (fig. 50). A primary bundle is a cylindrical mass, bounded externally by a structureless envelope, the sarcolemma. Its contents consist of fine fibrils, which, closely parallel to one another and pressed closely together, run from one end of the mass to the other. Each fibril is formed of singly and doubly refractive parts, which alternate with one another in more or less complicated arrangement. Since now the doubly refracting parts of the fibrils within a bundle lie at about the same level, there is caused a cross-striation extending through the whole bundle. Finally, scattered here and there between the muscle-fibrils are the muscle-corpuscles, spindle-shaped protoplasmic bodies with a nucleus, the remnants of the cells which have formed the musculature.

4. Nervous Tissue.

Function of Nervous Tissue.—As the muscular tissue brings about motion, so the nervous tissue serves for the transmission of stimuli. It communicates the stimulations of the sense-organs at the periphery to the central nervous system, the seat of consciousness, and here brings about perception (centripetal nerve tracts); further, it transmits the voluntary impulses to the periphery, particularly to the musculature (centrifugal nerve tracts). By the nervous system, finally, the stimuli arising in various places are co-ordinated, thus furnishing the elements for that which we call independent psychic activity.

Elements of Nervous Tissue.—The agent of the transmission of stimuli is undoubtedly a specific nerve-substance different from protoplasm. Hence we speak of nerve fibrillæ as of muscle fibrillæ, the product of the special nerve-cells, but the relations involved are not sufficiently understood.

The elements of the nervous system are divided into *ganglion cells* and *nerve-fibres*, but it must be remembered that these are not independent of each other, but that the fibres are enormously elongated processes of the ganglion cells. In the vertebrates the ganglion cells vary greatly in size; besides small elements there are large cells, only exceeded by the eggs in size, which correspondingly have large nuclei recalling the germinal vesicles. Unipolar, bipolar, and multipolar ganglion cells are recognized, the differences depending upon the number of processes (nerve-fibres) which arise. In multipolar cells the number is very large (fig. 51) and are of two kinds, dendrites and axons or neurites. *Dendrites* are so called because they branch again and again, not far from their origin from the cell. The *axons* (of which there is usually but one to a ganglion cell) can be followed to a long distance without giving off branches, except here and there lateral side twigs (collaterals) which arise at right angles to the main fibre; they often pass over into peripheral nerves. They branch at their tips, so the morphological distinction from dendrites lies in the greater distance of the region of branching from the body of the ganglion cell. In bipolar ganglion cells both processes are neurites, the cell itself thus being an element intercalated in the course of a nerve-fibre, as also is a unipolar ganglion cell. The single process of this divides near the cell in a T-shaped manner, so that the unipolar cell is to be regarded as a bipolar ganglion cell in which the two neurites are united for a short distance.

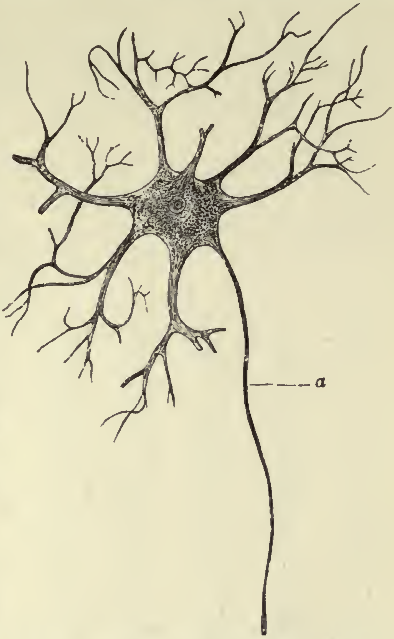


Fig. 51.—Multipolar ganglion cell of man. (After Gegenbaur.) *a*, axon.

This conception is intelligible in the light of recent researches on the structure of the ganglion cell and its processes (fig. 52). Both consist of extremely fine fibrillæ, and inter- and perifibrillar substances cementing them together. Each process brings a bundle of

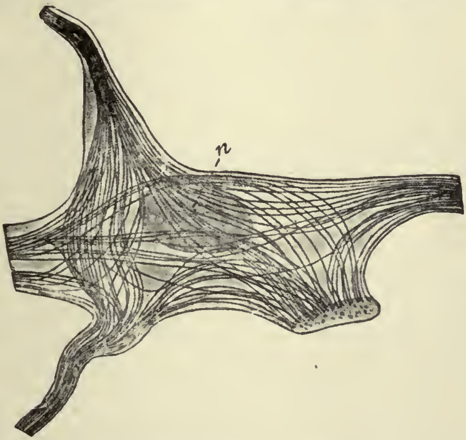


Fig. 52.—Motor ganglion cell from the thoracic region of the spinal cord of a dog. (After Bethe.) *n*, nucleus.

fibrillæ to the ganglion cell, in which they spread out and pass over into other processes. The branching of neurites and dendrites is a separation of the contained fibrillæ; the ganglion cell, the place of exchange of fibrillæ between the various processes. Hence the ganglion cell is not a simple cell, but a cell plus plasma products.

The similar fibrillar structure of nerve-fibres has long been known. In the central nervous system of vertebrates the most minute elements are the nerve fibrillæ, distinguished from muscle fibrillæ by the absence of cross-striation; from connective-tissue fibrillæ by the ease with which they are injured; in preserved material they frequently swell and show varicosities (fig. 53). Many fibrillæ united in a bundle form a nerve-fibre (fig. 54, *A*) which is called a *gray nerve-fibre* in distinction from the *white* or *medullated* fibres. In the latter the fibre or *axis-cylinder* is surrounded by a *medullary sheath* (fig. 54, *B*) composed of myelin, a fat-like substance, blackened by osmic acid and separated into variously shaped 'myelin drops.' The medullary sheath appears to act as an insulator.

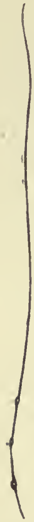


Fig. 53.

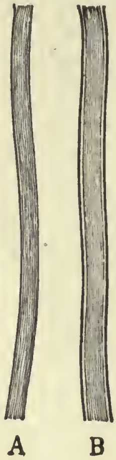


Fig. 54.

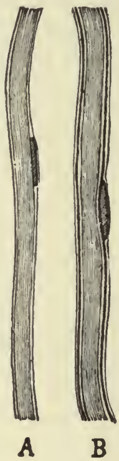


Fig. 55.

Fig. 53.—Nerve fibrillæ with varicosities. (From Hatschek.)
Fig. 54.—Non-medullated } nerve-fibres,
Fig. 55.—Medullated } *A*, without, *B*, with sheath of Schwann. (From Hatschek.)

Both medullated and non-medullated fibres can be enclosed in a 'sheath of Schwann.' This is a feature of the fibres composing the peripheral nervous system and is lacking in brain and spinal cord. It is a delicate envelope with nuclei here and there (fig. 55). At times it forms constructions which cut through the medullary sheath to the axis-cylinder (nodes of Ranvier).

Multipolar and bipolar ganglion cells also occur in the invertebrates, most commonly in the cœlenterates (fig. 56), more rarely in worms (e.g., *Lumbricus*), arthropods, and molluscs, and then chiefly in the peripheral nervous system. In the ganglia (the nervous centres of the last three groups) the ganglion cell usually gives rise to a single strong process, which, however, is richly provided with lateral branches or dendrites (fig. 74). The medullary sheath and sheath of Schwann are usually absent in invertebrates even in the peripheral nerves. A thin myelin layer has been rarely observed in arthropods and annelids. On the other hand the true conducting elements, the nerve fibrillæ, have been seen in invertebrate nerve-fibres, and these have been followed into the ganglion cell in which the afferent and efferent fibrillæ are united in a lattice-like manner.

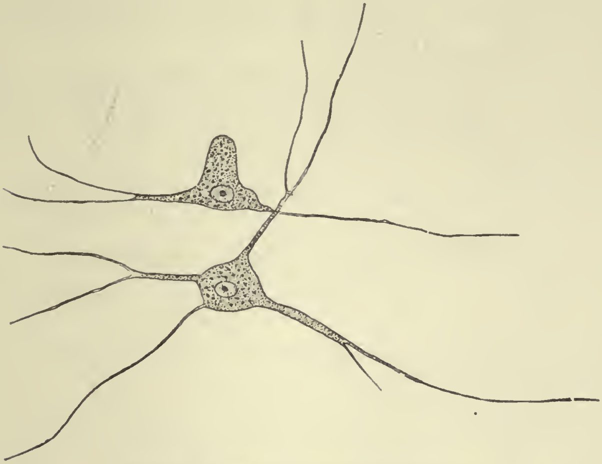


FIG. 56.—Ganglion cells of an actinian.

SUMMARY OF HISTOLOGICAL FACTS.

Cells.—1. The most important morphological element of all tissues is the cell.

2. The cell is a mass of protoplasm which contains one or several nuclei (uninucleated, multinucleated cells).

3. The nucleus probably determines the specific character of the cell, since it influences its functions; accordingly it is also the bearer of heredity.

4. Cells and nuclei increase exclusively by division or budding.

Tissues.—5. Tissues are complexes of numerous similar histologically differentiated cells.

6. Histological differentiation rests in part upon the fact that the cells take on a definite form and arrangement, in part upon the formation of plasmic products, which determine the character of the tissue (muscle-fibres, connective-tissue fibrils).

Classification of Tissues.—7. According to function and structure (1) epithelia, (2) connective tissue, (3) muscular tissue, (4) nervous tissue are distinguished.

8. The physiological character of *epithelia* is determined by the fact that they cover the surfaces of the body, their morphological character in that they consist of closely compressed cells united only by a cementing substance.

9. According to their further functional character epithelia are divided into glandular epithelia (unicellular and multicellular glands), sensory, germinal, and protective epithelia.

10. According to the structure are distinguished simple (cubical, cylindrical, squamous epithelia) and stratified epithelia, ciliated and flagellated epithelia, epithelia with or without cuticle.

11. The physiological characteristic of the *connective tissues* is that they fill up spaces between other tissues in the interior of the body.

12. The morphological distinction depends upon the presence of the intercellular substance.

13. According to the quantity and the structure of the intercellular substance the connective substances are divided into (1) cellular (scanty intercellular substance); (2) homogeneous; (3) fibrous connective tissue; (4) cartilage; (5) bone.

14. The physiological character of *muscular tissue* is its increased capacity for contraction.

15. The morphological characteristic is the fact that the cells have secreted muscle-substance.

16. According to the nature of the muscle-substance are distinguished smooth and cross-striated muscle-fibres.

17. According to the character and origin of the cells (muscle-corpuscles) the muscles are divided into epithelial (epithelial muscle-cells, primary bundles) and connective-tisue muscle-cells (contractile fibre-cells).

18. The physiological distinction of nervous tissue rests upon the transmission of sensory stimuli and voluntary impulses, and upon the co-ordination of these into unified psychic activity.

19. The conduction takes place by means of nerve-fibres (non-medullated and medullated fibrils and bundles of fibrils); the co-ordination of stimuli by means of ganglion-cells (bipolar, multipolar ganglion-cells).

20. *Blood* and *lymph* are proteid-containing fluids; rarely without cells, they may contain only colorless amœboid cells (white

blood-corpuscles, leucocytes), or in addition to these also red blood-corpuscles.

21. Red blood-corpuscles occur, in the main, only in vertebrates and cause the redness of the blood; they are absent in most invertebrate animals.

22. When invertebrate animals have colored blood (red, yellow), this is usually due to the color of the blood-plasma.

23. The red blood-corpuscles are nonnucleated in mammals, nucleated in all the other vertebrates.

III. THE COMBINATION OF TISSUES INTO ORGANS.

An Organ Defined.—Organs are formed from the tissues. *An organ is a tissue complex, marked off from the other tissues, which has taken on a definite form for carrying on a special function.* Thus a single muscle is an organ which consists of a certain amount of muscular tissue; with scalpel and scissors it can be removed from its environment as a connected whole and can still accomplish a definite movement.

Principal and Accessory Tissues.—In each organ there is a tissue which determines the function of the organ, and therefore its physiological character. This may be called the principal tissue, for there may be other accessory tissues present, which merely support or render possible the function of the principal tissue. In the muscle of the vertebrates we find, besides the muscle-fibres, connective tissue which, like a kind of cement, unites the bundles of muscle; blood-vessels which provide nourishment; finally, nerves by which the muscles are aroused to action. In the human liver also, besides the functionally most important part, the liver-cells, blood-vessels, nervous and connective tissues are present. These accessory tissues are usually found only in the highly developed organs; in the case of the lower animals they may be absent; thus the digestive tract of cœlenterates has only an epithelial lining; their nervous system consists merely of a cord of nerve-fibres and ganglion-cells.

Effect of Use and Disuse.—It is of the greatest importance for the permanency of an organ that it be constantly in function. Living substance is distinguished from the non-living by the fact that, if it be destroyed by use, it is immediately replaced, often by more than sufficient to make good the loss. Functioning tissues and organs under favorable conditions increase in volume; on the other hand, functionless parts undergo a gradual decrease, which finally leads to their disappearance.

Change of Function of Organs.—The two factors mentioned, that the permanence of the tissues depends upon continued use, and that usually several tissues enter into the structure of an organ, are important for the understanding of the principle of change of function which plays a prominent rôle in the metamorphosis of animal form. It may happen that an organ is brought under changed conditions and no longer has an opportunity to function as before. In that case the functioning tissue, from lack of use, gradually degenerates, but the organ may persist by means of its accessory tissues if the new conditions make it possible for one of them to attain to functional activity, and to give the organ a new physiological character.

Examples of Change of Function.—A muscle, for example, may become functionless from many causes. Should the muscle-tissue disappear there are still left the accessory tissues, particularly connective tissue permeated by blood-vessels; this may remain intact and form a protecting band, a tendon, or fascia. We have then, morphologically, the same organ, changed in its physiological character; the muscle has undergone a change of function, and has become a ligamentous band. The visceral arches of fishes afford another example; these primarily are supports for the gills; if now by the acquirement of terrestrial habits the gills be lost, the visceral arches become functionless and correspondingly undergo a partial degeneration; but a part persists by assuming a new function, and forms the jaws, the hyoid bone, and the small bones of the ear, which, in spite of their quite different functions, are morphologically the same structures as the gill-arches.

Homology and Analogy.—In the History of Zoology (page 14) it was shown that comparative anatomy has caused a discrimination between *homology* or morphological equivalence, and *analogy* or physiological equivalence, i.e., between organs which appear in the same relative positions and relations, and organs which have the same function. What we have here learned of the structure of organs makes it evident that morphological and physiological characters do not necessarily coincide, that morphologically similar organs may have different functions, morphologically different organs the same functions.

Systems of Organs.—Organs wholly identical, or, at least, functioning in an equivalent manner, may occur in considerable numbers in the same body. A man has many muscles, and many organs which carry on digestion. Hence we may group all organs which in the body have equivalent or similar functions, and speak of systems of organs. In all we recognize nine such systems: (1) skeletal, (2) digestive, (3) respiratory, (4) circulatory, (5) excretory, (6) genital, (7) muscular, (8) nervous, and (9) sensory systems. Not all are necessarily present; a skeleton, for instance, is frequently lacking. The most different functions which in man are divided among different complicated and specialized systems may be performed in a lower animal by one and the same apparatus. Yet according to the fundamental functions the following groups of organs may be recognized: I. Organs of assimilation (2–5); II. Organs of reproduction (6); III. Organs of motion (7); IV. Organs of perception (8 and 9).

Vegetative and Animal Organs.—The organs of assimilation and of reproduction (I and II) are grouped together as vegetative, the others (III and IV) as animal organs. The older zoologists used to say that assimilation and reproduction are functions which are common to animals and plants; that, on the contrary, sensation and motion are lacking in plants, and are exclusively characteristic of animals. The atom of truth in the fundamental idea needs reconsideration in the light of our present knowledge. We have seen that the protoplasm of plants and animals has not only the power of assimilation and reproduction, but also power of motion and of irritability. The latter characteristics consequently cannot be entirely lacking in all the plants, for they are found in the most important. In fact many plants, as the mimosas, the compass-plants, insectivorous plants show great irritability; many low plants, the reproductive states of algæ, move quite as actively as, or even more actively than, many of the lower animals. On the other hand, there are many animals which in the mature condition are fixed in position like plants. Many Protozoa and worms, most of the zoophytes, some echinoderms like the Crinoids, even many Crustacea, the cirripedes (barnacles), can change their location only during the earlier stages of development, in later life being limited to movements of single parts of the body, the arms, tentacles, etc. In the sponges motions are so insignificant that they cannot be seen at all by the naked eye, and scarcely even with the aid of the microscope.

Nevertheless the two terms, *animal* and *vegetative*, must be retained. For although motion and sensation occur in the vegetable kingdom, still they reach no high development; indeed we may say they become more and more inconspicuous the higher the plants; in the animal kingdom, on the contrary, they are unfolded in extraordinary perfection and lie at the basis of its most characteristic features.

Vegetative Organs.

A. *Organs of Assimilation.*

Assimilation Defined.—If the term assimilation be used in its widest sense, one must speak in this connection of all the contrivances in the animal body which render growth possible during the period of progressive development, and, during mature life, compensate for the loss of energy connected with each period of functional activity, in order to preserve to the body its functional powers. In each period of functional activity organic compounds are oxidized. Compounds which are especially rich in carbon and hydrogen (as well as some nitrogen and sulphur) and are poor in oxygen are changed by oxidation into carbon dioxide, water, and various nitrogenous products, like urea, uric acid, etc. A compensation takes place, for not only is the useless substance removed, but also compounds of oxygen and materials rich in carbon are furnished to the tissues to replace the material oxidized.

Assimilation in Animals.—In lowly organized animals all the processes connected with compensative assimilative changes take place through the agency of one and the same organ, the digestive tract; but in the higher animals, through specialization, normal assimilation is a definite series of separate phenomena. Between the lower and the higher animals there are evidently intermediate conditions where specialization has halted at an earlier or a later stage.

Different Organs of Assimilation.—Assimilation begins with the presence of suitable food; the solid and liquid constituent parts of the body must digest and incorporate this, i.e., it must be altered so that it can be absorbed and distributed to the tissues. All this takes place through the agency of the digestive tract, which is provided with accessory organs, the digestive glands; the digestive tract likewise removes all matter remaining undigested (the fæces). The necessary oxygen, gaseous food, so to speak, is usually taken, however, by particular parts of the body, the *respiratory organs,* the gills or lungs. The oxygen and the digested (consequently liquefied) organic and inorganic compounds must further be distributed in the body to the organs and tissues according to their needs. Therefore there are usually blood-vessels or *circulatory organs,* which permeate the body in all directions. But the tissues need not only a means of obtaining but also of getting rid of certain compounds. The accumulation of the oxidation products arising from functional activity is injurious, to some extent even poisonous, to the organism; consequently they must be removed, and in a dissolved state they are taken up by the blood-vascular apparatus, and are brought to definite places for expulsion or excretion. Fluid wastes are expelled by the kidneys of vertebrates, the Malpighian vessels of insects, the water-vascular system of worms; these, together with their accessory apparatus, are embraced under the name 'excretory organs.' *Excreta* are to be distinguished from *fæces;* excreta are substances which have been a part of the tissues of the body itself, and, through oxidation, have become useless; while those substances which constitute the fæces were useless from the beginning, and have never belonged to the body, but have remained separated from the tissues by the boundary of the epithelium of the digestive tract. The gaseous oxidation product of the animal body, carbon dioxide, is removed by the blood-vascular apparatus through the agency of the respiratory organs. Since in the respiratory organs there takes place an exchange of the useless carbon dioxide for the oxygen necessary to life, these organs have a double function, being, at the same time, excretory organs and organs for taking up food.

After this general survey, we must enter somewhat more minutely into a discussion of the various systems of organs.

I. The Digestive Tract.

Archenteron or Primitive Digestive Tract.—Since the taking in of food and its assimilation are functions most important for the well-being of the animal, it is to be expected that of all the organs in the animal series the digestive tract should be formed first, and also in almost every case should be earliest established in the embryo. The fact that many worms (cestodes) and crustacea (Rhizocephala) have no digestive tract does not alter this statement; for it can be definitely affirmed that, in adaptation to special conditions of life, particularly parasitism, the digestive tract has degenerated. The simplest multicellular, free-living animals are merely simple or branched digestive pouches which have only a single opening, functioning both as mouth and anus (fig. 57). Such an animal has necessarily two epithelial layers, one of which lines the digestive tract, the other covers the surface of the body. These two fundamental cell-layers are called entoderm and ectoderm. In many cœlenterates they are the only layers of the body. In most animals they are separated by intermediate tissues, called collectively mesoderm. The higher the animal, the more differentiated is the mesodermal layer. The primitive digestive cavity lined by entoderm is called the *archenteron*. In the case of medusæ and polyps it forms the entire digestive tract, but in most animals this is not sufficient for the needs of digestion and the alimentary tract is increased by invaginations of parts of the surface of the body.

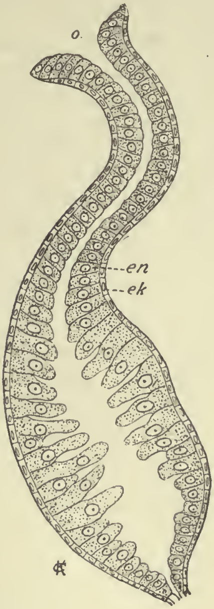


FIG. 57.

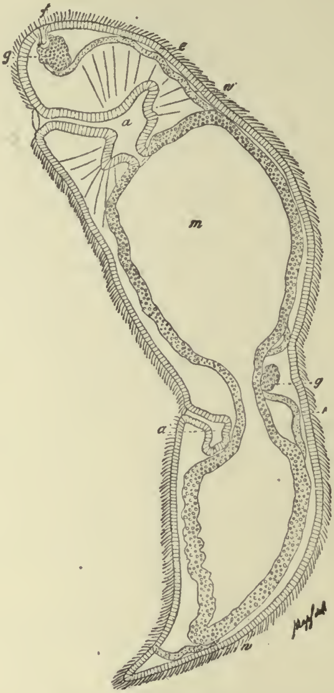


FIG. 58.

FIG. 57.—Longitudinal section through the nutritive polyp of a siphonophore. (After Haeckel.) o, mouth-opening; *en*, entoderm; *ek*, ectoderm.

FIG. 58.—*Stenostoma leucops*, in division. *a*, ectodermal fore-gut, at *a'* forming anew for the hinder animal; *m*, the blindly ending entodermal mid-gut; *e*, ectodermal ciliated epithelium; *g*, ganglion with ciliated pit; *w*, water-vascular canal; *g'*, ganglion of the hinder animal.

Stomodæum and Proctodæum.—Even in many cœlenterates and lower worms an invagination arises at the anterior end of the digestive tract, forming the ectodermal fore-gut or *stomodæum* (fig. 58). From the higher worms onwards, it is accompanied by a second invagination at the hinder end, the ectodermal hind-gut, or *proctodæum* (fig. 59); embryologically, this is formed as a blind sac whose closed end unites with the likewise closed posterior part of the archenteron (now called also *mesenteron* or mid-gut) until the separating wall disappears, whereupon mid- and end-gut communicate with each other, and the digestive tract becomes a canal extending through the entire body.

Divisions and Appendages of the Digestive Tract.—The part which the archenteron takes in comparison with the ectodermal proctodæum and stomodæum in making up the completed digestive tract is very different in the various groups. On one side the crustacea, on the other side the vertebrates, offer the strongest

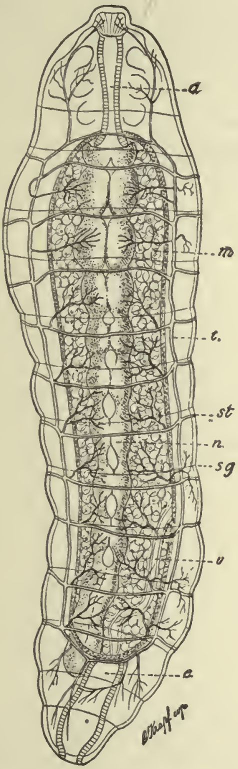


FIG. 59.

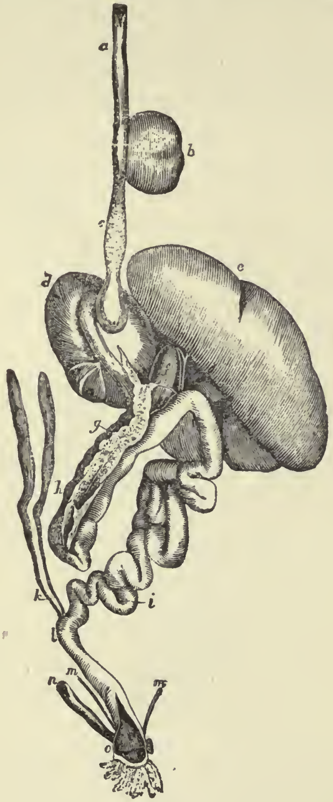


FIG. 60.

FIG. 59.—Bee-larva just after hatching: seen from the ventral surface. The digestive tract consists of three portions; *a*, fore-gut; *m*, mid-gut; *e*, hind-gut (not yet connected with the mid-gut); *sg*, limits of segments; *st*, stigma; *t*, trachea; *n*, ventral nerve-cord. (After Bütschli.)

FIG. 60.—Digestive tract of the domestic fowl. *a*, œsophagus; *b*, crop; *c*, glandular stomach; *d*, gizzard; *e*, liver; *f*, gall-bladder; *g*, pancreas; *h*, *i*, small intestine; *k*, cæca; *l*, large intestine; *m*, ureters; *n*, oviduct; o, cloaca.

contrast; the crustacea have a very short mid-gut and consequently a long extent of fore- and hind-gut formed from the ectoderm; in vertebrates, on the contrary, the ectodermal portions are extremely short.

The width of the lumen varies in the course of the alimentary canal and renders possible the distinction of different divisions, which, so far as possible, have been provided with uniform names. Fig. 60, drawn from a domestic fowl, illustrates the usual terms. The mouth-opening leads into a wider cavity, which is usually divided into an anterior division, the *buccal cavity,* and a posterior one, the *pharynx.* The narrow tube leading from this is the *œsophagus* (*a*); here and there it may widen, or bear a pouchlike evagination, the *crop* or *ingluvies* (*b*), for the temporary reception of food. From the œsophagus the food passes into a considerable enlargement, the stomach. Birds, like many other animals, have a double stomach, a thin-walled portion rich in glands, and a second part, the walls of which are remarkable for the thick masses of muscle; the former is the *glandular stomach* (*c*), the latter is the *grinding stomach* or *gizzard* (*d*), serving for comminution of the food. Behind the stomach the digestive tube narrows into the *small intestine* (*h*), the hinder widened part of which is the *large intestine* (*l*), terminating in the anus. The limit of the small and large intestine is usually marked by blind pouches, the *cæca* (*k*). Connected with the anal gut also are the outlets of the kidneys (*m*) and of the sexual apparatus (*n*); hence the terminal portion, serving as the outlet for the urine and fæces, and also for the sexual products, is called the *cloaca* (*o*).

In animals which require abundant food the area of the alimentary tract is not sufficient to furnish the digestive fluids, so that evaginations of the wall (glands) serve to increase this. Into the mouth empty the *salivary glands;* into the first part of the small intestine, close behind the stomach, the *liver* (*e*) and the *pancreas* (*g*) (or a single glandular apparatus, whose secretion combines the characters of gall and of pancreatic juice, the *hepato-pancreas*). Finally, in the hind-gut there sometimes occur glands which form a fetid secretion—the *anal glands.* The length of the digestive tract is chiefly influenced by the kind of food. In many groups of animals there is found a difference between herbivores and carnivores, the former having a very long and consequently convoluted digestive tract. That of a carnivore is about four or five times the length of the body, while in an herbivorous ungulate, on the other hand, it is twenty to twenty-eight times. Similar, though not so great, are the differences between carnivorous and plant-eating beetles.

II. Respiratory Organs.

Sources of the Oxygen used in Breathing.—The oxygen which each animal must obtain in exchange for the carbon dioxide formed in the tissues is derived either from the air or from the water, according as the animal is terrestrial or aquatic. Less frequently it is the case that water-dwellers breathe air, and hence are compelled, from time to time, to rise to the surface of the water for a supply of air; this is true for the great marine mammals, and for many insects, spiders, and snails which are found in fresh water. Air- and water-breathing takes place exclusively through the skin, so long as this is delicate and readily permeable, and so long as no higher development of organization necessitates a more active interchange of material. If, on the other hand, the demand for oxygen be greater, other more special breathing-organs are found —gills for water-breathing, lungs and tracheæ for air-breathing, in

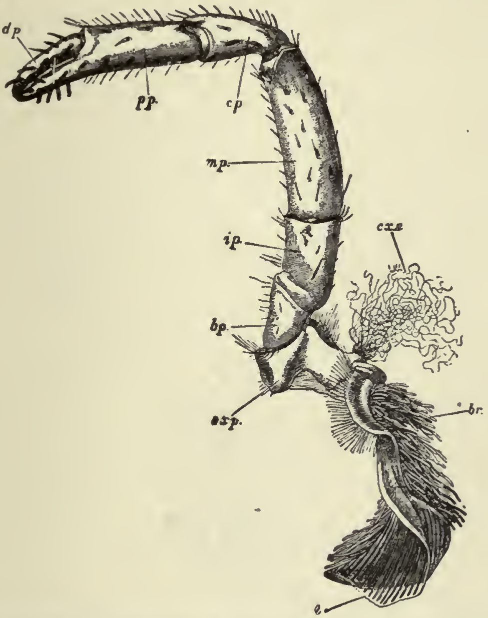


FIG. 61.—Left second foot of a crayfish with attached gill (*br*). (After Huxley.) *cxp*, coxopodite; *bp*, basipodite; *ip*, ischiopodite; *mp*, meropodite; *cp*, carpopodite; *pp*, propodite; *dp*, dactylopodite; *cxs*, bristles of the coxopodite; *e*, lamina of the gill.

addition to which the skin functions as an accessory organ of more or less importance.

Gills.—The gills are usually thin-walled areas of the skin which are abundantly supplied with blood-vessels, and where richly branched tuftlike projections or broad leaves have grown out, thus furnishing the largest possible surface for the interchange of gases; these occur in such a position as to be most exposed to fresh water; in the crayfish, for example, they are on the legs, where the motion drives fresh water constantly through them (fig. 61); in the swimming worms, on the back; in the tube-dwelling worms, at the anterior end, projecting out of the tube (fig. 62); in most amphibians (fig. 4), on each side of the neck. More rarely the digestive tract functions for water-breathing; in the fishes, Enteropneusta, and tunicates gills have been formed in connection with the pharynx, its lateral walls being pierced by the gill-slits, which open to the exterior on the surface of the body. The water containing oxygen in solution passes out through the gill-slits, and bathes the gill-filaments, which are richly provided with blood-vessels. The hind-gut also in many fishes, insects, and worms

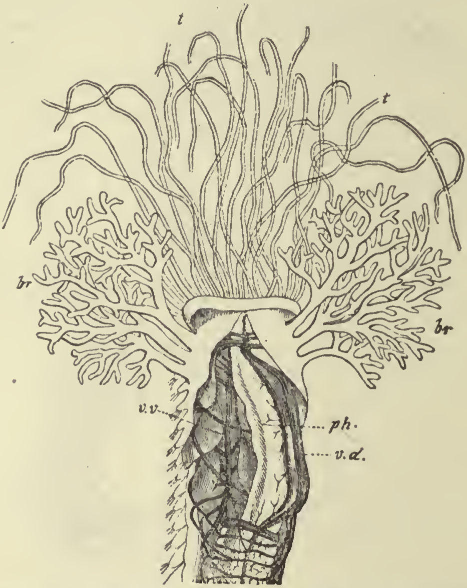


FIG. 62.—Anterior end of *Terebella nebulosa*. (After Milne Edwards.) *ph*, pharynx; *vd*, dorsal, *vv*, ventral, blood-vessel; *br*, gills; *t*, tentacles.

may become an accessory respiratory organ, being filled from time to time with fresh water.

Aerial Respiration.—In the air-breathing animals the respiratory apparatus is derived either from the digestive canal or from the skin. With the vertebrates the former is the case, since the lungs, either directly or by the mediation of the trachea and bronchi, are in connexion with the lumen of the digestive tract. On the contrary, in the case of invertebrate animals (snails and spiders) when the term 'lung' is used, it refers always to an invagination or sac of the skin; of such a nature are the tracheæ of insects, tubes containing air, beginning at the surface of the body with a hole or stigma, and branching internally (fig. 59, *st*).

Distinctions between the Respiratory Systems of Chordates and Invertebrates.—In general, then, a distinction can be drawn between the respiratory systems of vertebrate and invertebrate animals: in the former, the digestive tract, or derivatives from it, are respiratory; in the latter, on the contrary, it is the skin. On the side of the vertebrates the only exceptions are most amphibians and a few fishes (*Protopterus*), in which the gills are tuftlike projections of the skin (figs. 4 and 5); while among the invertebrates some aquatic insects respire by the hinder end of the digestive tract.

III. Circulatory Apparatus.

In order that the oxygen, taken up by the respiratory organs, and the constituents of the food digested in the alimentary canal may reach the tissues, there is no need of special organs, so long as the body consists of only two thin epithelial layers, the ectoderm and entoderm. When, however, a third, a mesodermal, layer is interpolated between these, and the body consequently becomes more bulky, there is usually some apparatus for distributing the food. The simplest is when the digestive tract departs from the character of a straight tube and branches, and by means of these branches extends into the various parts of the body. We speak then of a *gastro-vascular system,* because the alimentary canal itself takes on the function and the branching arrangement generally characteristic of the vessels or 'vascula' (fig. 63).

Cœlom.—The cœlom or enterocœle is apparently derived from a pair of gastric diverticula which have become completely cut off from the archenteron (compare development of mesoderm, *infra*). It is a cavity pushed in between the intestinal tract and the body-wall, is lined by a special epithelium, the *peritoneum,* and encloses most of the vegetative organs. If the two halves of the cœlom approach, without uniting, dorsal and ventral to the gut, the result is dorsal and ventral membranes, the *mesenteries*, which support the alimentary canal. Of these the ventral is most frequently, the dorsal least often, degenerate. In many invertebrates the cœlom plays an important rôle in nutrition since it contains a lymphoid fluid, rich in proteids and containing cellular corpuscles. It loses this significance the more the blood system is developed, and in the vertebrates, so far as nutrition is concerned, it is a rudimentary organ.

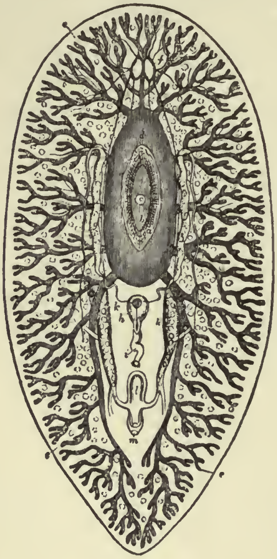


FIG. 63.

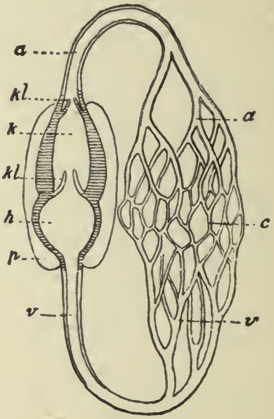


FIG. 64.

FIG. 63.—*Leptoplana tremellaris.* *a*, mouth; *b*, buccal cavity; *c*, opening of the head of the pharynx into the buccal cavity; *d*, central stomach; *e*, branched entodermal gut; *f*, ganglion; *g*, testicle; *h*, seminal vesicle; *k*, uterus; *l*, receptaculum seminis; *m*, female sexual opening.

FIG. 64.—Schema of circulation of the blood. *a*, arteries; *c*, capillaries; *h*, auricle; *k*, ventricle; *kl*, valves; *p*, pericardium; *v*, veins.

A sharp distinction should be drawn between the cœlom and other cavities in the body. Not every 'body cavity' is a cœlom, but frequently there occur large spaces which are entirely different in origin and in relations. Frequently, as in arthropods, these 'body cavities' contain blood and are in reality but expansions of the vascular system. To such cavities the term *hæmocœle* has been given.

Heart, Arteries, Veins, Capillaries.—The most complete method of food distribution is accomplished by the *blood-vessels*, which, therefore, belong generally to the higher animals, and function whether a body cavity is present or not. Blood-vessels are tubes with fluid contents, the blood, which transports the oxygen received through the respiratory organs, as well as the food absorbed from the digestive tract, and later gives these up to the tissues. Since such an interchange of substances presupposes that the blood circulates in the vessels, definite parts in the course of the blood-vessels are contractile; they are covered by muscles which by their contraction narrow the tube and push the fluid forwards. In the lower forms wide areas in the course of the blood-vessels are contractile; in higher animals a greater regularity of circulation is reached; a definite specialized muscular part of the course, the *heart,* alone propels the blood.

The Higher Development of the Heart.—A free motion of the heart is only possible when it is separated from the contiguous tissues and enclosed in a special cavity (fig. 64). Hence we see that the heart always lies either free in the body cavity or enclosed in a special pouch (*p*), the *pericardium* (in all cases a portion of the general body cavity, but not always of the cœlom, which has become independent). The division of the heart into a part which receives the blood, the *atrium* or *auricle* (*h*), and a part which drives the blood onward, the *ventricle* (*k*), is of less functional importance; hence this division is not carried out in all cases. There are also special mechanisms within the heart, the valves (*kl*), which, by closing, prevent the blood from flowing back when the walls relax at the end of the contraction.

Blood-vessels.—In order that the blood system may properly perform its function, in addition to circulation, it is necessary that the nutritive substances be readily taken up and given out again to the tissues. The part of the course of circulation concerned in this must have easily permeable walls, must be widely distributed in the body, and have a large superficial area. These demands are met by the *capillaries* (*c*), extremely fine and thin-walled tubes, which surround and permeate all organs. Through their walls, usually formed of a thin epithelial layer alone, the proteid substances for nourishing the tissues can pass, and the oxygen can be exchanged for carbon dioxide. Between the heart and the capillaries there exists, corresponding to their different functions, great differences in structure; they must therefore be united by special transitional vessels—vessels which begin large and thick-walled at the heart, and by branching, and thinning of their walls, pass gradually into the capillaries; of such vessels there are two kinds, the firmer *arteries* (*a*) leading to the capillary region, and the thinner-walled *veins* (*v*) leading back to the heart.

Correlation of Respiratory Organs and Blood System.—It is a law that in all animals the blood-vascular system has been influenced in its arrangement and structure more by respiration than by nutrition in the narrower sense; there exists a correlation between the organs of respiration and of circulation. A double capillary region must be distinguished; besides the body capillary system already mentioned there is the respiratory capillary region, whose exclusive office is to remove the carbon dioxide from the

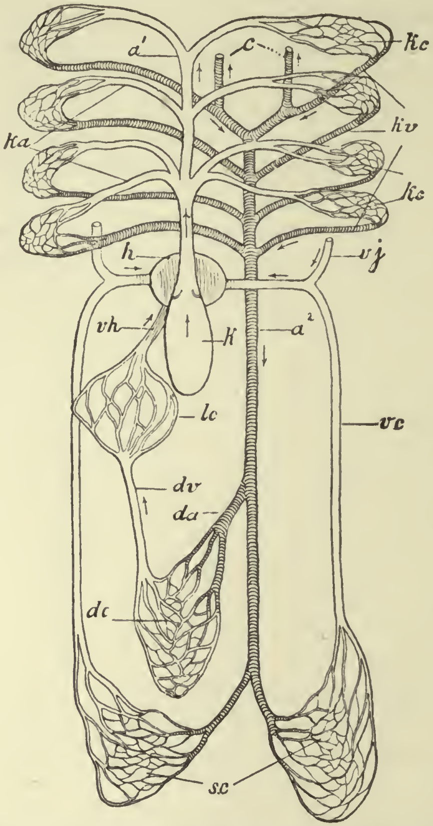


FIG. 65.—Scheme of circulation in a fish. *a'*, ascending (ventral) aorta; *a²*, descending (dorsal) aorta; *c*, carotid, *da*, intestinal arteries; *dc*, intestinal capillaries, *dv*, intestinal veins; *h*, auricle; *k*, ventricle; *ka*, afferent gill-arteries; *kv*, efferent gill-arteries; *lc*, liver-capillaries; *sc*, body-capillaries; *vc*, cardinal veins; *vh*, hepatic vein; *vj*, jugular vein.

blood and to furnish oxygen to it (gill and lung capillaries). A twofold capillary region makes necessary also a twofold system of arteries and veins (systemic arteries and systemic veins, respiratory arteries and respiratory veins). The accompanying diagram (fig. 65) of the blood circulation of fishes illustrates this. Veins lead from the capillary region of the tissues of the body to the auricle of the heart; from the auricle the blood flows into the ventricle, and through the afferent gill-arteries into the gill-capillaries. Thence it is conducted through the 'gill-veins' (efferent arteries), which unite into a single large trunk; this again gives off lateral branches passing into the capillary region of the body. Since the branches of the main trunk formed by the 'gill-veins' lead again into a capillary region, they must, like the main stem, be called arteries.

Arterial and Venous Blood.—During its course through the body the blood twice changes its chemical character and correspondingly its color. The blood which flows from the body capillary region has given up its oxygen to the tissues, receiving in exchange carbon dioxide, and has become dark red. This character is maintained until, in the gill-capillaries, it again becomes oxygenated, giving up the carbon dioxide and becoming bright red. The different character of the blood can be recognized in the arteries and veins of the systemic circulatory system; the dark blood containing carbon dioxide is called *venous,* and the bright red, containing oxygen, *arterial* blood, since the former flows in the veins, the latter in the arteries. These terms are entirely unsuitable, as can readily be seen from the above diagram (fig. 65), because they easily lead to the false assumption that veins must always conduct blood containing carbon dioxide, and arteries always oxygenated blood. In opposition to this, the diagram shows that, in the respiratory circulation (the shorter course), the conditions must be the reverse of those in the systemic circulation, since here the arteries contain 'venous,' while the veins contain 'arterial,' blood.

Closed and Lacunar Blood-vascular Systems.—Such a blood-vascular system as has here been described is called a *closed* one, because the blood always flows in special tubes provided with their own walls. Opposed to the closed stands the *lacunar blood-vascular system;* here the blood-vessels lose, after a time, the character of tubes and become wide cavities, or sinuses, which, without special walls, are enclosed between the intestines and other organs (hæmocœle, *supra*).

Example of Lacunar Blood-vascular System.—The best example of a lacunar blood-vascular system is furnished by the insects and myriapods, which have only the heart and short arterial trunks; from the ends of the arteries the blood enters the hæmocœle, and from this through lateral slits (ostia) again enters the heart (fig. 66). In the groups of arthropods and molluscs are found all transitions between so extreme a case of a lacunar blood-vascular system and the almost completely closed one. Here appears again a close *correlation of the circulatory and respiratory organs,* the latter determining the development of the former. If the respiration be diffusely distributed over or through the body, and the distribution of the oxygen goes on without special vessels, the circulatory apparatus is very simple; on the other hand, if the respiration be connected with definitely restricted areas, and a regular distribution of oxygen be necessary, the apparatus is differentiated into heart, arteries, veins, and capillaries. Details may be found in the sections on crustaceans, spiders, and insects, *infra.*

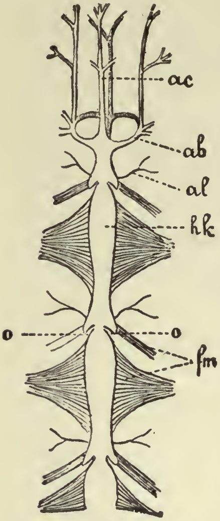


FIG. 66.—Anterior end of the heart of *Scolopendra.* (After Newport.) *ac*, cephalic artery; *ab*, arterial arch; *al*, lateral artery; *fm*, alary muscles (alæ cordis); *hk*, chambers of heart; *o*, ostia.

Lymph-vessels.—A special part of the vascular system is the *lymph system,* which is known only in vertebrates. In the capillary region of the body, it is true, proteids may pass over into the tissues, but it is evident that a possible overflow cannot re-enter the blood-vessels in the same way, on account of the higher pressure prevailing in the capillaries. This overflow is conducted back to the veins through the lymph-vessels. The lymph-vessels begin with lacunæ in the tissues, and gradually pass into vessels with definite walls. The lymph-vessels of the digestive tract are particularly important since, during digestion, they become filled with the proteid and fatty constituents of the digested food; they are called the *chyle-vessels,* because they contain the chyle, distinguished from ordinary lymph by its milky color.

Cold- and Warm-blooded Animals.—In connexion with the blood-vascular system, two expressions are much used but not generally correctly understood by the general public, viz., cold-blooded and warm-blooded—or, more correctly, animals with *variable* and animals with *definite temperatures.* Under the head of animals with varying temperature (poikilothermous) or cold blood are placed forms whose temperature is largely dependent upon the temperature of the environment, rising and falling with it, but usually a few degrees above it. In our climate, where the atmospheric temperature is considerably lower than the temperature of the human body, such animals, for example the frog, would feel cold to our touch, since they, particularly in the cool season, have a much lower temperature than we.

Such creatures as, living under any thermal condition, maintain about the same temperature, are termed warm-blooded or definite-temperatured (idiothermous, homoiothermous) animals. Man in summer and winter, under the equator and at the north pole, has approximately a temperature of 36° C. ($98\frac{2}{5}$° F.), showing higher temperatures only in fever. In order to maintain a constant temperature during the varying external conditions, the animal must have a heat-regulator; it must have the power to regulate the warmth of its body, on the one hand by limiting the production of heat, on the other by controlling its loss. If the environment be warmer than is suitable for the body temperature, then the production of heat must be limited to the smallest quantity compatible with the vital processes; but, if this does not suffice, the loss of heat must be increased by evaporation from the surface, usually accomplished by active perspiration. If, on the contrary, the environment be cold, then, conversely, every unnecessary loss of heat must be avoided, while the production of heat must be increased. It is clear that idiothermy, since it requires complicated apparatus, can occur only in the highly organized animals.

IV. Excretory Organs.

Nature of the Organs of Excretion.—The excretory organs are tubes or glandular canals which open upon the surface of the body, either directly or by way of an end-gut (cloaca), and conduct substances which have become useless to the body to the exterior.

The presence of a blood-vascular system or a cœlom or both together exercises an important influence on their structure. When neither are developed the excretory tubules in order to remove the excreta from the tissues must branch and penetrate the body in all directions like a drainage system, being frequently connected in a network recalling the blood-capillaries (*protonephridia* or *water-vascular system* of parenchymatous worms, fig. 67). The canals begin with closed tubes, which are provided internally at the end with a bundle of actively vibrating cilia, the 'flame' (fig. 68). One or more main trunks lead from the canal system to the exterior. A little before the external opening (excretory pore) there is frequently a contractile enlargement, the urinary bladder.

With the appearance of a cœlom there is a central place for the collection of excreta. The *nephridia* or segmental organs — usually simple tubes (rarely branched) open at both ends—lead from this to the exterior. One opening is external (fig. 69), the other communicates with the cœlom by means of a ciliated funnel, the *nephrostome,* a wide mouth with active cilia which connects with the canal of the tube. Through this the excretion (in annelids peritoneal cells laden with guanin—the disintegrated 'chloragogue' cells) is carried to the outside.

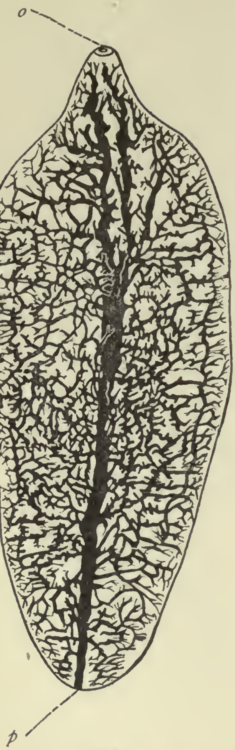


FIG. 67.

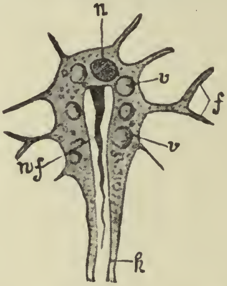


FIG. 68.

FIG. 67.—*Distomum hepaticum* with water-vascular system. (From Hatschek.) *p*, porus excretorius; *o*, mouth.

FIG. 68.—Blind end of one of the finest water-vascular canals (*k*) of a Turbellarian. (From Lang.) *n*, nucleus; *f*, processes of the terminal cell; *wf*, 'flame' of the terminal cell; *v*, vacuole.

The excretory organs (kidneys) of vertebrates are derived from such nephridia. The fact that in the embryos (and frequently in the adults) these open into the cœlom by nephrostomes makes it probable that also in the vertebrates the cœlom was once important in excretion (fig. 70). The increasing importance of the blood-vessels which envelop the nephridial canals and bring to them the waste matter taken from the tissues is probably the cause of the loss of connexion of the kidneys with the cœlom by degeneration of the nephrostomata. The relation of the blood-vessels to the nephridial tubes becomes specially close by the development of the glomeruli (Malpighian corpuscles); bundles of capillaries carrying the walls of the canal before them and so projecting into the lumen of the tube.

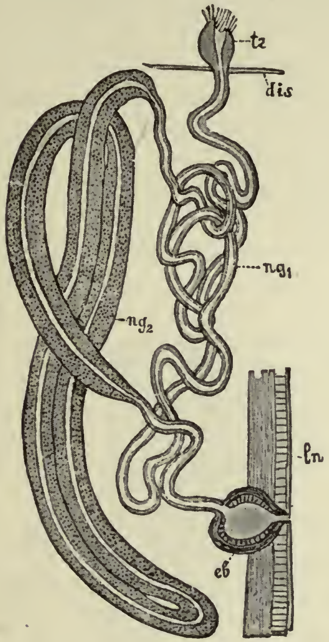


FIG. 69.

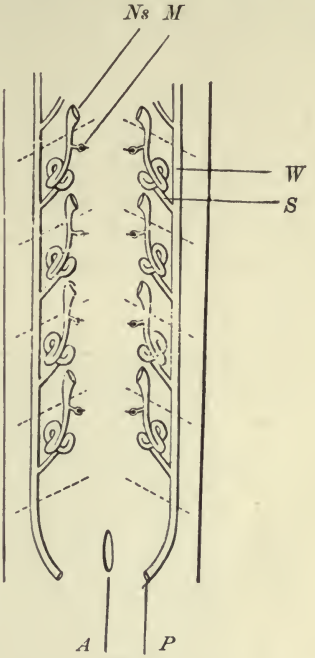


FIG. 70.

FIG. 69.—Segmental organ of an Oligochæte. (From Lang.) *tz*, ciliated funnel; *dis*, septum; ng^1, non-glandular, ng^2, glandular, part of the canal; *eb*, terminal vesicle; *ln*, body-wall.

FIG. 70.—Diagram of the primitive kidney of a vertebrate. (From Hatschek.) Dotted lines mark the limits of the segments. *A*, anal opening; *P*, mouth of the duct of the primitive kidney (*W*); *Ns*, nephrostome; *M*, Malpighian bodies of the segmental tubules (*S*).

B. *Sexual Organs.*

Sexual Glands and Ducts.—In the sexual apparatus of animals are distinguished the areas where the germinal cells are produced, the *sexual glands* or *gonads,* and the ducts for these. The former are present, temporarily or permanently, in all multicellular animals; the latter, on the contrary, may be completely absent. If the sexual products arise in the skin or in the walls of the digestive tract, as is usually the case in the cœlenterates, then special outlets are superfluous, since the ripe elements can reach the exterior directly by rupture of their covering or by means of the digestive tract.

Germinal Epithelium and Germinal Glands.—Male and female sexual cells, as we have seen, originate from an undifferentiated incipient organ, or anlage, which is called the germinal epithelium. Usually it forms a part of the epithelial lining of the body cavity, in many animals permanently, in others only temporarily; in the latter case it separates, usually by constriction, and forms gland-like bodies, the gonads or sexual glands.

Gonochorism and Hermaphroditism.—In most animals the germinal epithelium produces either only female or only male sexual cells; such animals are called separate-sexed, *diœcious* or *gonochoristic*, in opposition to the *hermaphroditic* forms, in which both kinds of sexual glands are contained in one and the same individual. Different degrees of hermaphroditism can be distinguished; commonly testes and ovary are contained in the same

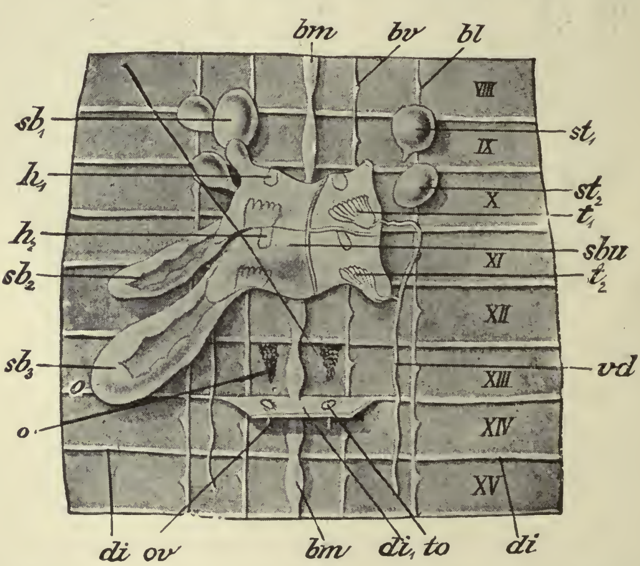


FIG. 71.—Sexual organs of *Lumbricus agricola*. (From Lang, after Vogt and Yung.) The seminal vesicles of the right side are removed. *bm*, ventral nerve-cord; *bv* and *bl*, ventral and lateral rows of setæ; st^1, st^2, receptacula seminis; sb^1, sb^2, sb^3, the three seminal vesicles of the left side, which are connected with a median unpaired seminal capsule (*sbu*). Enclosed in the latter are the anterior and posterior testes (h^1, h^2), and the anterior and posterior seminal funnels (t^1, t^2), which lead into the vas deferens (*vd*). *o*, ovaries; *to*, ciliated funnels leading into the oviducts (*ov*); *di*, dissepiments; VIII–XV, eighth to fifteenth segments.

animal, some distance apart, as in the earthworm, in which two segments are male, while a third segment is female (fig. 71). More rarely there is a union of testes and ovary into a single glandular body or hermaphroditic gland; our land-snails have an hermaphroditic gland, which produces spermatozoa and eggs in the same follicle.

Occurrence of Hermaphroditism. — Hermaphroditism is, in general, of more frequent occurrence in the lower than in the higher animals. Insects and vertebrates are, almost without exception, diœcious; only two cases of normal hermaphroditism are known among them, a sea-perch, *Serranus scriba,* a bony fish, and *Myxine glutinosa,* the hagfish. More commonly hermaphroditism occurs as an abnormality; a striking form is lateral hermaphroditism, in which one half of the animal has only male, the other half only female, gonads. If the males and females of a species be distinguishable by their appearance, then lateral hermaphroditism is expressed in their external form, since one half of the animal has the characteristic marks of the male, the other half those of the female. Hermaphroditic lepidoptera and bees are known in which the male half bears the special form of the male antennæ, eyes, and wings, and thus is essentially different from the female half (fig. 72). Still it must be noted here that, in many instances where the external appearance pointed towards hermaphroditism, anatomical investigation has disclosed either only male or only female sexual glands in a rudimentary condition (gynandromorphism). True hermaphroditism (the presence of both kinds of sexual glands in the same animal) is extremely rare in mammals and in man. What is described as hermaphroditism does not in the majority of cases deserve the name.

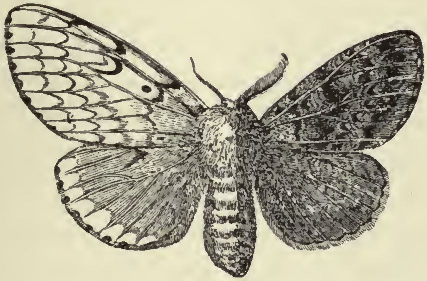


FIG. 72.—Lateral hermaphroditism of a gipsy moth (*Ocneria dispar*). Left female, right male. (After Taschenberg.)

Genital Ducts.—Very frequently in the animal kingdom the excretory apparatus furnishes outlets for the sexual products. In the annelids and in the vertebrates portions of the nephridial system, either exclusively or in addition to their excretory function, become accessory sexual organs. Hence we speak of a *urogenital system.* This remarkable connexion of genital and excretory organs has a double cause, a physiological and an anatomical. Physiologically important is the fact that eggs and spermatozoa behave like excreta; being substances which are no longer destined for the use of the individual, but must reach the exterior in order to become efficient. The morphological cause is the relation to the cœlom. A urogenital system is formed only in animals in which the germinal epithelium arises from the epithelium of the cœlom, and in which the kidneys or their rudiments stand permanently in connexion with the body cavity and thus form the natural outlet for its products. Whether the accessory sexual parts are portions of the excretory organs or are independent structures, they have in the animal series a definite arrangement adapted to their function (fig. 73). Canals lead from the sexual glands to the exterior, the *oviducts* in the female, the *vasa deferentia* in the male (and the hermaphroditic duct from the hermaphroditic gland).

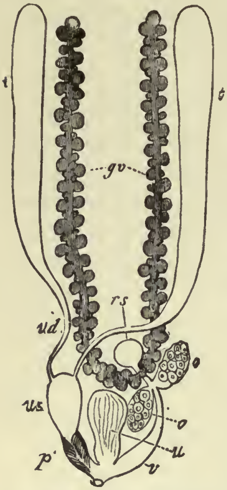


FIG. 73.—Sexual apparatus of *Vortex viridis.* (From Gegenbaur, after M. Schultze.) *t*, testis; *vd*, vasa deferentia; *vs*, vesicula seminalis; *p*, penis; *o*, ovary with oviduct; *u*, uterus; *v*, vagina; *rs*, receptaculum seminis; *gv*, yolk-glands.

Accessory Sexual Apparatus.—The terminal portion of the vas deferens is often very muscular and is called the *ductus ejaculatorius;* it may be evaginated as a *penis* or *cirrus,* or project permanently beyond the surface of the body. The terminal portion of the oviduct is often widened so that two portions may be distinguished, the *uterus,* which harbors the eggs during their development, and the *vagina,* which serves for copulation. In addition there may occur in both sexes other accessory glands of the most diverse character. Oviduct and vas deferens may be provided with sac-like evaginations which serve for the reception of the sperm. In the female these are called *receptacula seminis,* in the male *vesiculæ seminales;* the former give lodgment to sperm which enters the female sexual passages during coition, the latter to sperm which has been formed in the testes of the same individual.

Animal Organs.

I. Organs of Locomotion.

Voluntary Locomotion.—The power to change their location voluntarily is a peculiarity so prominent in animals that to the general public it is sufficient for deciding whether an organism belongs to the vegetable or to the animal kingdom. On this account it is necessary to call attention to the fact that numerous animals lose the power of locomotion, becoming fixed to the ground, to plants, or to other animals. All sponges and corals, most hydroid polyps, and the crinoids among the echinoderms, have actively swimming larvæ, but become fixed in the adult and thus obtain such a marked similarity to plants that, although true animals, they were long regarded as plants. Further, many molluscs and worms are firmly fixed by their shells; indeed, many crustacean forms, the cirripeds, have completely lost their free motility. But a more careful investigation in all these cases will show that the power of moving the separate parts exists, for the corals can retract their tentacles, the cirripeds their featherlike feet, and the clam can close its shell.

Locomotion among Lower Animals.—The lowest forms, the Protozoa, progress almost exclusively by processes of the cell: *pseudopodia, cilia,* or *flagella.* In the metazoa this is rarely the case. Amœboid movements of the epithelial cells, indeed, occur in the cœlenterates and also in many worms, but do not suffice for change of position. More effective is the ciliated or flagellated epithelium, by which ctenophores, turbellarians, and rotifers swim; this occurs, besides, in many larvæ of animals which, in the mature state, are unable to change their location or do so only by the aid of muscles. Nearly all cœlenterates, echinoderms, molluscs, and the majority of the worms leave the egg-membranes in the form of the planula, i.e., as a larva swimming by means of cilia.

Locomotion among Higher Animals.—The *musculature* is alone adapted for energetic motions. The arrangement of this varies with and depends upon the constitution of the skeleton. Forms without a skeleton have commonly the 'dermo-muscular tunic,' a sac of circular and longitudinal muscle fibres which is firmly united with the skin. If a skeleton be formed by the skin, as in the arthropods, then the sac breaks up into groups of muscles, which find points of attachment upon the dermal skeleton; if, on the other hand, as in the vertebrates, an axial skeleton be formed, a fixed point is furnished for muscular action, so that the musculature obtains a quite new character, in particular a deeper position. A locomotor apparatus quite unique is the *ambulacral system* of the echinoderms, a system of delicate little tubes with protrusible portions which function as feet, described in connexion with that group.

II. Nervous System.

Scarcely a system of organs in the animal series shows such a regular development as the nervous system. The different stages which can be grouped may be termed the diffuse, the linear, the ganglionic, and the tubular types.

Diffuse Nervous System.—The diffuse type is certainly the most ancestral; it shows the two elements, nerve fibres and ganglion cells, regularly distributed through the whole body, or, at least, through certain layers of the body. The skin of the body, the ectoderm, is to be looked upon as one of the fundamental elements in the nervous system, since it is related to the external world, and hence receives the sensory impressions, so important for the development of nervous tissue. The corals and hydroid polyps are examples, since in them the ectoderm is permeated in all directions by a delicate, subepithelial spider-weblike network of nerve fibres and ganglion cells, which encroach even upon the entoderm.

Linear Nervous System.—From the diffuse type the other chief types can be derived through concentration, which is chiefly conditioned by the fact that there are a few points which are most advantageously located for the reception of sensory stimuli, and hence for the development of nervous elements. In the medusæ such a place is the rim of the bell; consequently a stronger nerve-cord remarkably rich in ganglion cells is found here. This, as well as the nerve-ring and the five ambulacral nerves of echinoderms, may be called a *central system*, thereby distinguishing the rest of the nervous network as the *peripheral nervous system.*

Ganglionic Central Nervous System.—Numerous transitional forms lead to the *ganglionic* central nervous system of the worms, molluscs, and arthropods (fig. 74). The central nervous system here consists of two or more ganglia; each ganglion being a rounded bunch of regularly arranged nerve-fibres and ganglion-cells. The former constitute the centre of the mass, and, since they cross in all directions, give the appearance of fine granulations; this fact has led to the unsuitable, because misleading, name of 'Leydig's dotted substance.' The ganglion-cells, on the other hand, collect in a thick layer around the dotted substance. The peripheral nerves, and also the *commissures*, the cords connecting similar ganglionic masses, extend outwards from the ganglia.

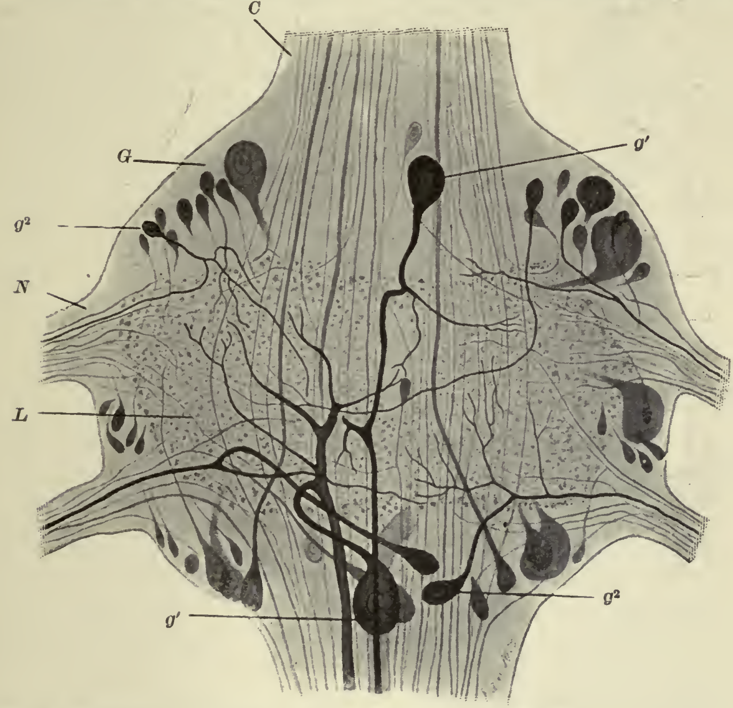


Fig. 74.—Third abdominal ganglion of a crayfish. (After Retzius.) *C*, connective or longitudinal commissure; *G*, ganglion cell layer; *g'* ganglion cell whose neurites enter the connective; *g*², ganglion cell whose neurites enter the peripheral nerve; *L*, Leydig's dotted substance; *N*, peripheral nerve.

Supraœsophageal (or Cerebral) Ganglia.—Since most animals are symmetrical, the ganglia occur in pairs; left and right ganglia correspond to one another and are connected simply by a cord of nerve-fibres, the transverse commissure. Of most constant occurrence are two ganglia, which lie dorsally above the pharynx, and hence are called the *supraœsophageal* or *cerebral ganglia*. If other ganglia occur, they lie ventrally and below the digestive tract (ventral nerve-cord).

Ladder Nervous System.—A widely recurring arrangement is that termed the *ladder nervous system* (of annelids and arthropods) (fig. 75). Numerous pairs of ganglia (in the example before us, nine) lie in serial order on the ventral side of the animal, and are connected by longitudinal commissures (connectives), and also by transverse commissures connecting the left and right ganglia. The first pair of the series is formed by the infra-œsophageal ganglion, which sends out commissures right and left, surrounding the pharynx, to the supra-œsophageal ganglion. The supra- and infra-œsophageal ganglia together with the œsophageal commmissures form the *œsophageal ring,* a nerve-ring surrounding the œsophagus.

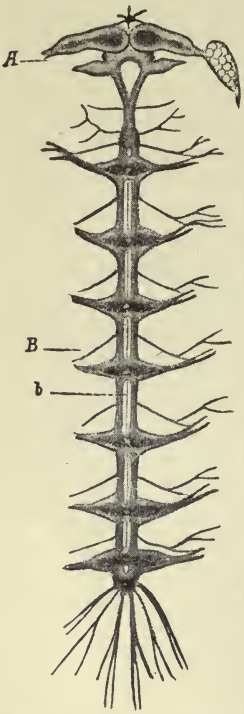


Fig. 75. — Ladder nervous system of *Porcellio scaber* (sowbug). (After Leydig.) *A*, brain; *B*, ventral cord, connected with the brain by the œsophageal commissures; *b*, a cord formerly regarded as sympathicus.

Tubular System.—The tubular type of nervous system is found only in the chordates (fig. 76). The vertebrate brain and spinal cord may be regarded as parts of a tube with greatly thickened walls, developed in different ways. In the centre lies the extremely narrow central canal, which widens anteriorly into the several ventricles of the brain. In a transverse section the nervous elements are seen grouped around the central canal in a manner almost the reverse of that of the ganglionic type. On the periphery lies a layer of nerve-fibres (the 'white matter' of human anatomy); next is a central portion formed of ganglion-cells and nerve-fibres (the 'gray matter'), which is marked off from the central canal by a special epithelium (ependyma).

Relations between the Nervous System and the Skin.—For almost all animals it has been ascertained that *the nervous system arises from the ectoderm.* Therefore, in many animals, the nerve-cords and the ganglionic masses lie pemanently in the skin; in others only during the development, later becoming separated by splitting off or by infolding, and thus coming to lie in the deeper layers of the body (fig. 9).

III. Sensory Organs.

Sensations of the Lower Animals.—What we know of the character of the external world is founded upon experiences gained through our sensory organs. We thus know the external world only in so far as it is accessible to the senses, controlled by the judgment. If things exist outside of ourselves which have no influence upon our senses, we can form no conception of them. It follows from this proposition that we can gain knowledge of the natural capacity of the sensory organs of animals only by analogy with our own experiences. Hence the distinction of five senses, touch, taste, smell, hearing, and sight, based upon human physiology has been extended to the whole animal kingdom. *A priori,* however, it cannot be denied that sensations may occur in animals which we do not experience; following out this course of thought has led to the idea of a 'sixth sense,' which, however, must remain to us a meaningless abstraction, since it is impossible for us to conceive of the character of a sense which we lack.

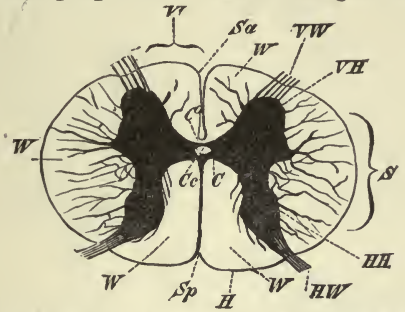


Fig. 76.—Cross-section of the human spinal cord. (From Wiedersheim.) Black represents the gray, white the white substance of the cord ; *Cc*, central canal, surrounded by the anterior and posterior commissures (*C* and *C′*); *Sa*, *Sp*, anterior and posterior fissures ; *VW*, *HW*, anterior and posterior nerve-roots ; *VH*, *HH*, anterior and posterior horns of gray matter; *V*, *S*, *H*, anterior, lateral, and posterior columns of white matter.

Anatomy gives Insufficient Knowledge of Sensory Organs.—A further, and still more important reason for our very fragmentary knowledge of animal sensations is the fact that, in regard to the physiological meaning of the sensory apparatus, it is seldom that we can depend upon experiments, and consequently we must base our conclusions upon structure. But the anatomy of many sensory organs, like those of smell and taste, is by no means so characteristic that it alone is sufficient to determine the physiological significance.

Tactile Organs.—The skin of animals functions as a tactile organ, usually over the whole area, although not everywhere with equal intensity. Prominent parts, like the tentacles of polyps and of many worms, the antennæ of arthropods and the snails, need only mention. Special epithelial cells with stiff hairs projecting above the surface, the tactile bristles or tactile hairs, are tactile (fig. 77). Only in the vertebrates do the nerves of touch terminate in specially modified end organs (Vater-Pacinian corpuscles, corpuscles of Meissner, etc., fig. 78); these usually lie under the epithelium.

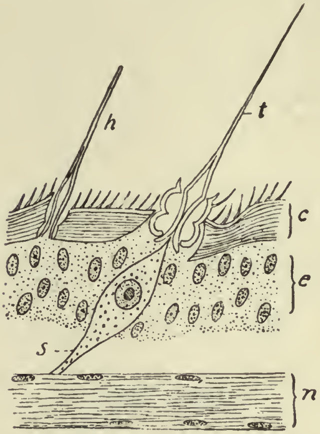


Fig. 77.

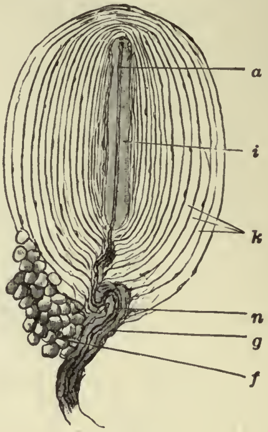


Fig. 78.

Fig. 77.—Skin of an insect with an ordinary hair (*h*) and a tactile hair (*t*); *n*, nerve; *s*, sensory cell; *e*, epithelium; *c*, cuticle. (After vom Rath.)

Fig. 78.—Vater-Pacinian corpuscle of the mesentery of a cat. *a*, axis cylinder; *f*, fat; *g*, blood-vessel; *i*, inner bulb; *k*, capsule with nuclei; *n*, medullated nerve-fibre.

Organs of Smell and of Taste are accurately known only in vertebrates. The olfactory organ of fishes consists of two small pits in the skin, above or in front of the mouth.

In the air-breathing vertebrates this pair of pits which here also arise from the skin are taken into the dorsal wall of the two respiratory canals leading from the outside to the pharynx. Now since the olfactory cells distributed in these pits (fig. 37, *β*) are frequently characterized by bundles of olfactory hairs, while the surrounding epithelium is often ciliated, one is inclined to regard as organs of smell sensory organs of invertebrates (e.g., medusæ, cephalopods), which have the form of ciliated pits and lie near the respiratory apparatus (e.g., the osphradium of molluscs). Yet there are exceptions. Experiments seem to show that in the arthropods the antennæ probably serve for smelling. Here the sensory perception can be connected only with certain modified hairs, the olfactory tubules of the Crustacea and the olfactory cones of insects. In a similar way certain nerve end organs in the region of the mouth are considered as organs of taste, since the taste organs of vertebrates, the so-called taste buds, are abundant in the mouth cavity, especially on the tongue.

Organs of Hearing and of Sight are called the higher sense-organs, because they are of much greater importance for the totality of our perceptions than the other organs, since they furnish sensations which are quantitatively and qualitatively much more definite. Ears and eyes have therefore a complicated and characteristic structure, which renders them easily recognizable by the almost invariable presence of certain structures accessory to their functions.

History of the Auditory Organs.—The auditory organs of vertebrates and of most of the other animal groups can be traced back to a simple fundamental form, the *auditory vesicle* (fig. 79).

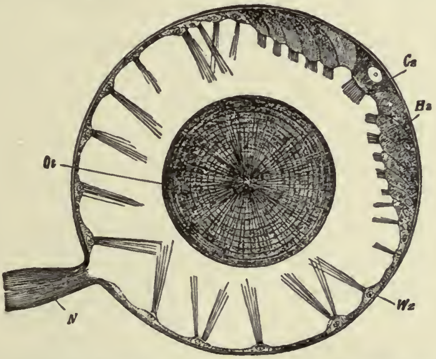


Fig. 79.—Auditory vesicle of a mollusc (*Pterotrachea*). *N*, auditory nerve ; *Hz*, auditory cells with the central cell, *Cz* ; *Wz*, ciliated cells ; *Ot*, otolith. (After Claus.)

This has an epithelial wall, a fluid contents, the *endolymph*, and an auditory ossicle or *otolith*, formed from a single or from several fused auditory concretions. In some instances the otoliths, to the number of thousands, may remain separate. In a definite region of the epithelial wall the cells are developed into the *crista acustica*, the auditory ridge; they are in connexion with the auditory nerve and bear the auditory hairs projecting into the endolymph. The otoliths themselves are concretions of carbonate or of phosphate of lime (exceptionally in *Mysis* of fluoride of calcium). They usually float free in the centre of the vesicle, and are often held in place by bundles of cilia which project from the non-sensitive epithelial cells.

Auditory Pit.—Every auditory vesicle develops from a pitlike invagination of the skin, and consequently is for a time an auditory pit. Therefore it is not surprising that in many animals the organ has stopped at the lower stage of development; for example, the crayfish has an open auditory pit. On the other hand, the auditory vesicle may develop a complicated system of cavities as in mammals (fig. 80), where it is divided by a constriction into the sacculus and the utriculus. The sacculus is provided with a spirally-wound blind sac, the cochlea, the utriculus with the three semicircular canals. In addition there is formed in the mammals, as also in most vertebrates, a sound-conducting apparatus, so that the auditory organ acquires an extremely complicated structure.

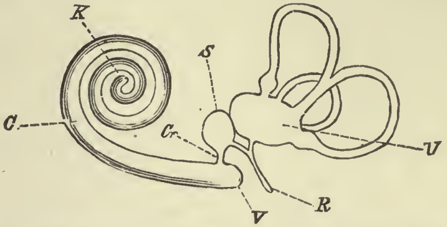


Fig. 80.—Diagram of the human labyrinth. *U*, utriculus with the semicircular canals; *S*, sacculus connected with the cochlea (*C*) by the canalis reuniens; *R*, recessus labyrinthi; *V*, blind sac of the cochlea; *K*, apex of the cochlea.

Other Forms of Auditory Organs.—Since there are animals without auditory vesicles which hear well, like the spiders and insects, we must assume that there are auditory organs which are formed after another type. Still we have no certain knowledge of these except in the case of the tympanal auditory organs of the grasshoppers (which compare).

Function of the Semicircular Canals. — Experiments upon representatives of the most diverse classes of vertebrates have led to the conclusion that the three semicircular canals, standing at right angles to each other, are organs of equilibrium, for, after these canals are destroyed, the animals begin to stagger and lose their balance. It is probable that in fishes this is the sole function of the labyrinth; for it has not been determined that fishes hear. Starting from this assumption, recent investigators have attempted to prove that the auditory vesicles of invertebrated animals are exclusively, or at least largely, organs of equilibration. This would explain the otoliths, for these bodies, of relatively large specific gravity, would affect the crista in different ways according to the position of equilibrium of the body. Statoliths would thus be a better name.

The Eye is in all animals recognized by the character of the sensory epithelium, the *retina.* This always has a large amount of pigment which lies either in the sensory cells or in special cells arranged between or behind them. The simplest-formed eye, therefore, appears as a sharply circumscribed pigment-spot in the epithelium of the skin, provided with nerves, commonly also with a lens (fig. 81).

Rods and Cones.—The sensory cell itself bears usually at its peripheral end a process, the rhabdom. This is a cuticular structure, probably serving to collect the rays of light and thus to stimulate the cell, and has, particularly in the vertebrates, a complicated structure, each rhabdom consisting of an inner and an outer portion. Here can be frequently distinguished two kinds of rhabdoms, rods and cones (fig. 82).

The Optic Ganglion.—Before the optic nerve divides into the separate visual cells it forms a swelling, the *optic ganglion,* which either lies as a detached body outside of the eye, or is united with the retina into a connected whole. The

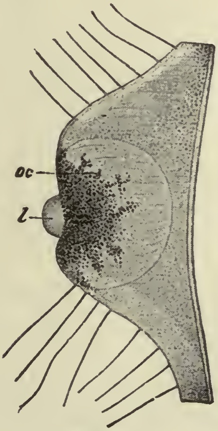


FIG. 81.

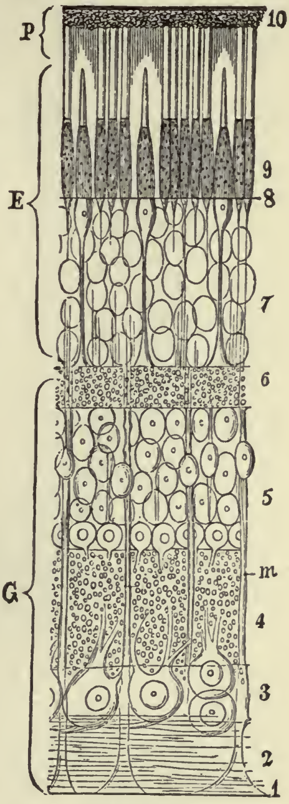


FIG. 82.

FIG. 81.—Ocellus (*oc*) of a medusa (*Lizzia koellikeri*) with lens (*l*).

FIG. 82.—Human retina. (After Gegenbaur.) P, pigment-layer; E, layer of sensory cells; G, optic ganglion; 1, limitans interna; 2, nerve-fibre layers; 3, ganglion-cells; 4, inner reticular layer; 5, inner granular layer; 6, outer reticular layer; 7, outer granular layer; 8, limitans externa; 9, rods and cones; 10, tapetum nigrum; *M*, Müller's fibres.

considerable thickness of the vertebrate retina is due to the fact that it includes the optic ganglion. The parts (fig. 82) called reticular layers, inner granular layer, ganglion cells, and nerve-fibre layer, constitute the optic ganglion; the layer of visual cells consists only of the outer granular layer and the connected rods and cones. The outer granules are the nuclei of the visual cells to which rods and cones belong.

Accessory Structures.—The eye may be further complicated by special refractive bodies (cornea, lens, vitreous body) which concentrate the light in order to cast an image upon the retina; and an iris to regulate the amount of light. Then, too, means for nutrition (the choroid coat) and for protection (sclerotic coat) must be provided. If all these parts be present, a structure results such as is found in the squid and in the vertebrates (fig. 83).

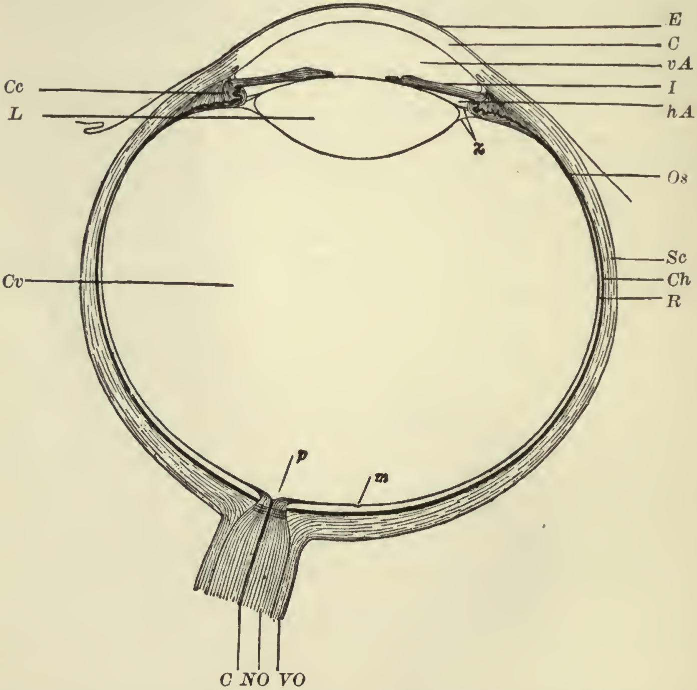


FIG. 83.—Horizontal section through the human eye. (After Arlt, from Hatschek.) *E*, epithelium of the cornea (conjunctiva); *C*, cornea; *vA*, anterior chamber of the eye; *I*, iris; *hA*, posterior chamber of the eye; *Z*, zonula Zinnii; *Os*, ora serrata; *Sc*, sclerotic coat; *Ch*, choroidea; *R*, retina; *p*, papilla of optic nerve; *m*, macula lutea, area of most distinct vision; *VO*, sheath of the optic nerve; *NO*, optic nerve; *C*, arteria centralis; *Cc*, corpus ciliare; *L*, lens; *Cv*, vitreous body.

The Eye of the Vertebrates.—The eye of the vertebrates usually is an approximately spherical body whose surface is formed by a firm membrane. Over the greater part of the circumference this is an opaque, fibrous or cartilaginous covering, called the sclera, or *sclerotica;* it is transparent only in the most anterior part, and here it forms by its greater convexity a projecting portion like a watch-glass, the *cornea.* Internally to the sclera lies the *choroidea,* an envelope of connective tissue, rich in pigment and blood-vessels, which, at the junction of sclera and cornea, is changed into the iris. The iris, the seat of the color of the eye, is pierced in the centre by the pupil, an opening the varying size of which regulates the amount of light. Next internal to the choroid follows a layer of black cells, the *tapetum nigrum* (pigmented epithelium), and finally the *retina* itself, the expansion of the optic nerve which enters the eye at the hinder part. The tapetum nigrum and the retina arise together, and hence both end at the edge of the pupil, although the retina loses its nervous character at the ora serrata, some distance from the outer edge of the iris.

The cavity of the eye is completely filled by the *vitreous body, aqueous humor,* and the *lens.* For vision the lens is the most important, since, next to the cornea, it influences most the course of the rays of light. It lies behind the iris, fixed to the anterior wall of the choroidea, which here is changed into the ciliary process. In front of it is a serous fluid, the aqueous humor, partly in the so-called posterior chamber of the eye, between the lens and iris, partly in the anterior chamber, between the iris and cornea. The single, larger cavity behind the lens is filled up by a jelly-like mass of tissue, the vitreous body. The image formed on the retina is inverted.

The Various Types of Eyes.—Between the simple pigment-spot and the highly organized vertebrate eye are many transitional stages: pigment-spots with lens and vitreous body, with enveloping and nourishing coverings, etc. The faceted eye of insects and Crustacea shows a special type of development, described later under the Arthropoda.

SUMMARY OF THE MOST IMPORTANT POINTS OF ORGANOLOGY.

1. Organs are composed of tissues, and by their environment are led to the formation of a body of definite shape and to the performance of a single function; consequently every organ is

characterized morphologically (according to its structure and its relations) and physiologically (according to its function).

2. Organs of different animals may be *physiologically equivalent*, *analogous* organs (i.e., with similar functions).

3. Organs of different animals may be *morphologically equivalent*, *homologous* (developing in similar relations).

4. In the comparison of the organs of two animals three possibilities become evident.

a. They may be at the same time homologous and analogous.

b. They may be homologous, but not analogous (swim-bladder of fishes, lungs of mammals).

c. They may be analogous, but not homologous (gills of fishes, lungs of mammals).

5. Organs are divided into *animal* and *vegetative.*

6. *Animal* functions are those which are not completely foreign to plants, but are only slightly developed in them; in the animal kingdom, on the contrary, they undergo an increase and become characteristic.

7. *Vegetative* functions are developed with equal completeness, though in a different manner, in plants and animals.

8. To the animal organs belong the organs of motion and sensation, such as the muscles, the sense-organs, the nervous system.

9. To the vegetative organs belong the organs of nutrition and reproduction.

10. Under *nutrition,* in the widest sense, are included not only the taking in and digestion of food and drink, but also the taking in of oxygen (respiration), the distribution of food to the parts of the body, and the removal of matter which has become useless.

11. With nutrition, therefore, are concerned not only the digestive tract and its accessory glands, but also the organs of respiration, the blood-vascular system, and the excretory organs (kidneys).

12. The male and female sexual organs serve for reproduction.

13. The male and female organs may occur in different individuals (*diœcious*), or both may be found in one and the same animal (*hermaphroditic*).

14. The highest degree of hermaphroditism is attained when one and the same gland (the hermaphroditic gland) gives rise to both eggs and spermatozoa.

15. Very often the sexual organs and the ducts from the kidneys are closely united; we then speak of a urogenital system.

IV. Promorphology, or Study of the Fundamental Forms.

Organic and Inorganic Bodies.—The structure of the individual animal rests upon the regular combination of differently-functioning organs. The organs thus assume a relation to one another which is definite for each animal group, or varies only in subordinate ways. If the various groups be compared with reference to the principle of the arrangement of parts, there appear a few fundamental forms which play a rôle in morphology similar to that of the fundamental forms of crystals in mineralogy. But we must not carry this comparison too far, and attempt to compare the study of the fundamental forms, the *promorphology*, of animals with crystallography as of equal value. A crystal is a mass made up of similar parts; its form is the necessary and immediate result of the chemico-physical constitution of its molecules. A direct connection of this kind between molecular structure and fundamental form does not, and cannot, exist in the organism, since each organ is composed of many chemical combinations. Consequently there is lacking also the mathematical regularity which occurs in crystals. Even in the case of animals which have the greatest regularity in the arrangement of their parts there is not an entire conformity to the demands of the fundamental form, so that we are compelled to ignore certain greater or less variations. If, for example, we call man bilaterally symmetrical, we overlook not only the slight asymmetry of a nose awry, etc., but also what is more important—that the liver has been pushed to the right,

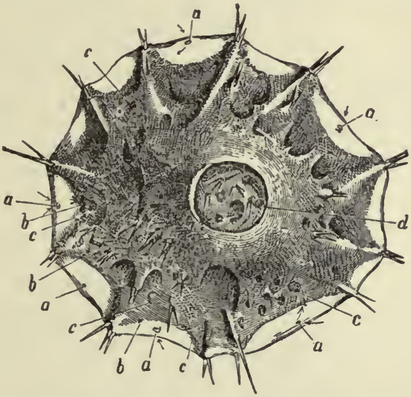


Fig. 84.—*Spongilla fluviatilis*, fresh-water sponge. (After Huxley.) *a*, superficial layer with dermal pores; *bc*, region of the ampullæ; *d*, osculum.

the heart to the left; and that the digestive tract throughout its entire course runs asymmetrically.

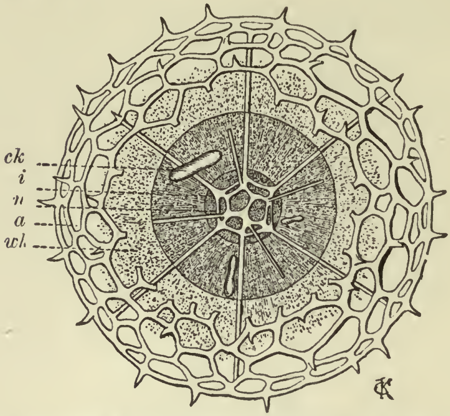


Fig. 85.—*Haliomma erinaceus*, a radiolarian. *a*, external, *i*, internal, latticed spherical skeleton; *ck*, central capsule; *wk*, extra capsular soft parts; *n*, nucleus.

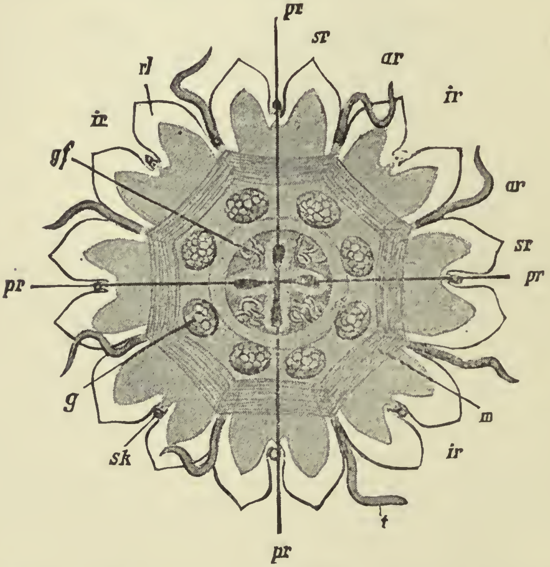


Fig. 86.—*Nausithoë*, an acraspedote medusa (after Lang), seen from the end of the greatly shortened main axis. *pr*, perradii; *ir*, interradii; *ar*, adradii (perradii and interradii mark the four planes of symmetry of the animal); *sr*, subradii; *rl*, mantle-lobes; *t*, tentacles; *sk*, sensory organs: *g*, sexual organs; *gf*, gastric filaments; *m*, subumbrellar circular muscle; in the centre the cross-shaped mouth-opening.

Symmetry.—Now, according to the three dimensions of space, we can pass three axes, perpendicular to each other, through the body of an animal, and up to a certain degree may characterize it according to the nature of these axes; further, we may characterize it according to the planes by which it can be symmetrically halved, the planes of symmetry. Thus we find the following fundamental forms:

1. Anaxial, asymmetrical, irregular, or amorphous fundamental form (fig. 84).
2. Homaxial, symmetrical in all directions, spherical fundamental form (fig. 85).
3. Monaxial, radially symmetrical (fig. 86).
4. Simple heteraxial, biradially symmetrical (figs. 87, 88).
5. Double heteraxial, bilaterally symmetrical (fig. 89).

1. *Anaxial* or *asymmetrical* animals, so called, are those in which the arrangement of parts is not regularly defined in any direction or space, and they therefore may grow irregularly in any direction. There is no fixed central point, and there is no possibility of running *definite* axes through the body or of dividing it into symmetrical parts. (Many sponges and many Protozoa.)

2. *Homaxial* or *spherical* animals have the sphere as their fundamental form; the parts of the body are arranged concentrically around a fixed central point, so that any number of axes and planes of symmetry can be passed through it; that is to say, all lines and planes which run through the central point of the sphere. (A few spherical Protozoa, chiefly radiolarians.)

3. *Monaxial* or *radial symmetry* is brought about, if growth go on in a definite direction, and correspondingly also if the formation of organs take place in directions other than perpendicular to this. The line which marks this direction of growth is the main axis, in distinction from the accessory axes or radii, which are all similar to each other. The main axis can be determined, because it is longer or shorter than the accessory axes; but it may also be of the same length and still be entirely distinct, since it contains certain organs (e.g., the mouth-opening) which are lacking in the other planes. In radially symmetrical animals the same organs are always present in greater number and are distributed regularly around the main axis in the direction of the radii. Through such an animal a great number of sections can be made, which pass through the long axis and halve the body symmetrically. If we cut the animal in the direction of all the possible planes of symmetry, we obtain pieces which, in essential points, are similarly con-

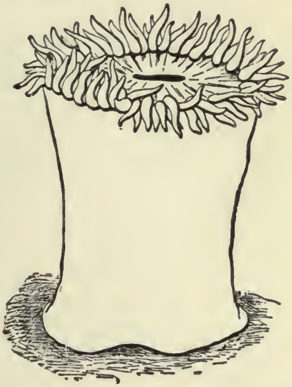


FIG. 87.—Diagram of an actinian (after Andres, from Hatschek). Side view, perpendicular to the much-lengthened main axis.

structed. Great groups of animals, as most echinoderms and cœlenterates, are more or less completely radially symmetrical.

4 and 5. The next two fundamental forms have in common the fact that three unequal axes perpendicular to each other are distinguishable; these may be designated as the main axis, the transverse axis, and the sagittal axis: this is the case if, leaving the main axis out of consideration, an arrangement of organs occur different in the sagittal direction from that in the transverse direction—if organs lie in the former which are lacking in the latter or the reverse. There are then, if we take into consideration the dissimilarity of the axes, two possible planes of symmetry: the animal can be symmetrically divided, (1) if the division passes through the main and transverse axes, (2) if it passes through the main and the sagittal axes. Such *biradially symmetrical* animals are the ctenophores, actinians (figs. 87, 88), and corals.

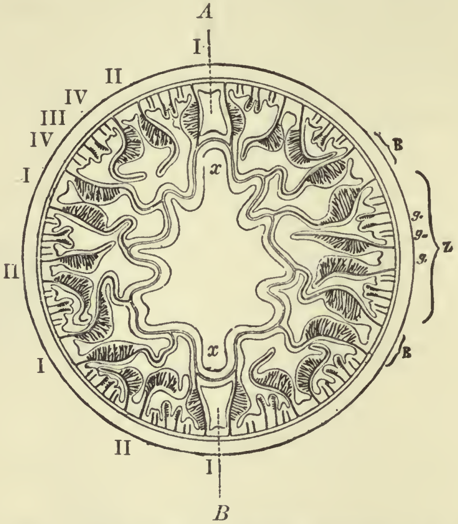


FIG. 88.—Cross-section of an actinian (*Adamsia diaphana*). *AB*, directive septa, which are at the same time ends of the sagittal axis, which marks one plane of symmetry of the body, while the second stands perpendicular to it; *I-IV*, circles of paired septa of first to fourth order.

Bilateral Symmetry.—If now we further suppose that the ends of the sagittal axes become unlike, that at one end are organs quite different from those of the other, we then reach the most usual form, *bilateral symmetry*. The dissimilar ends of the sagittal axes are called 'dorsal' and 'ventral,' and further the terms 'right' and 'left' are given to the ends of the transverse axis; a bilaterally symmetrical animal can be divided symmetrically into a right and a left half by one plane, the median, passing in the direction of the longitudinal sagittal axis; a frontal section (a section through the longitudinal and transverse axes) always gives dissimilar parts, dorsal and ventral sides.

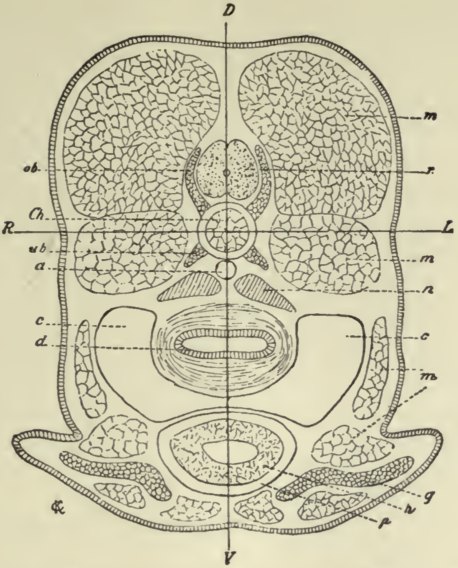


FIG. 89.—Cross-section of a fish passing through the fore limbs. *DV*, sagittal axis; *RL*, transverse axis; *a*, dorsal aorta; *c*, body cavity; *d*, gut; *ch*, notochord; *g*, shoulder-girdle; *h*, heart; *m*, muscles; *n*, anterior end of the kidneys; *p*, pericardium; *ob*, neural arch; *ub*, hæmal arch; *r*, spinal cord.

Antimeres and Metameres.—The symmetrical parts of an animal are called *antimeres;* each antimere has organs which occur likewise in its adjacent antimere. The right arm of man corresponds to the left, the right eye to the left, etc; the same organs are repeated in the direction of the transverse axis. Frequently, however, the repetition of organs occurs not only in the direction of the transverse axis, but also in the direction of the long axis. Thus the body is made up not only of symmetrical parts, the antimeres, but also of similar parts placed one behind the other, the *metameres.*

Internal and External Metamerism.—Metamerism or *segmentation* is spoken of when the body of an animal consists of numerous segments or metameres (consult fig. 59). Very often it is recognizable externally—when, for instance, the limits of the segments are marked on the surface by constrictions (arthropods and annelids). But this *external metamerism* may be entirely lacking, and the metamerism find expression only *internally* in the serial succession of organs, in metameric or segmental arrangement. Man, for example, is segmented only internally; in his skeleton there are numerous similar parts, the vertebræ, which follow one another in the long axis. In fishes the musculature also is made up of numerous muscle segments, as any one can readily see by examining a cooked fish. In the case of the externally segmented earthworm also, the ganglia of the nervous system, the vascular arches, the nephridia or segmental organs, the setæ, and the septa of the body cavity are repeated metamerically.

Homonomous and Heteronomous Metamerism.—The examples mentioned are well adapted for illustrating the different forms, the *homonomous* and the *heteronomous*, of metamerism. The earthworm is homonomously metameric, because the single segments are much alike in structure, and only slight differences exist between the anterior, the posterior, and the genital segments. Man and all vertebrates, on the contrary, are heteronomously metameric, because the successive segments, in spite of many points of agreement with one another, have become very unlike. The segments of the head have an importance, for the organism as a whole, quite different from those of the neck, the thorax, or the tail. A division of labor has taken place among the segments of an heteronomous animal.

Heteronomy and Homonomy.—The distinction between heteronomy and homonomy is of great physiological interest. The more different the segments of an animal become the more dependent they are upon one another in order to be able to function normally; so much has the whole become unified that the single parts can live only while the continuity is maintained. On the contrary, if the connexion between the parts be less intimate, they are more similar, and the more able to exist after separation from one another. This is most beautifully shown in instances of mutilation. It has been observed that when many species of Lumbricidæ are cut in two each part not only lives on by itself, but it even regenerates the part which is lacking; if, on the other hand, the same thing is done to a heteronomously segmented animal, either death immediately ensues, as in the case of the higher vertebrates, or the parts live for a short time a hopeless existence, as can be seen in the case of frogs, snakes, insects, etc. In metamerism a phenomenon is repeated which obtains widely in the animal kingdom, and contributes towards its higher development; first there is a reduplication of parts, then a division of labor, so that the final result is a whole composed of many parts, yet uniformly organized.

II. GENERAL EMBRYOLOGY.

Origin of Organisms.—Since the development of every individual begins with an act of generation, the ways by which new organisms may arise should be mentioned first in this chapter. If we wish to limit ourselves to that which has been actually observed, we must still cling to the old expression of the renowned Harvey, "Omne vivum ex ovo," and modifying it somewhat say, Omne vivum e vivo: that every living organism is derived from another living organism. We must limit ourselves to the mode of origin which has been termed tocogony, or generation by parents. The great importance which the question of generation without parents, or spontaneous generation, has obtained through the evolution theory renders a consideration of this question necessary at this point.

I. Generatio Spontanea, Archegony.

Theory of Spontaneous Generation.—The old zoologists, even Aristotle himself, believed that many animals, including even highly organized forms, like frogs and most insects, arose by spontaneous generation from the mud. Not until the seventeenth and eighteenth centuries did this doctrine find energetic opponents, in Spallanzani, Francesco Redi, Rösel von Rosenhof, Swammerdam, and others, who endeavored to prove experimentally that all animals lay eggs which must be fertilized by the spermatozoon in order to develop further. By their convincing investigations the doctrine of spontaneous generation was driven into the realm of the lower animals. Here it found a new foundation in the occurrence of parasites inside of animals which, at the beginning of their life, without doubt must have been free from these internal inhabitants. Parasitologists maintained that the parasites arose quite anew from the superfluous plastic material of their host. At last, by a series of epoch-making researches, the way was discovered by which the young of the parasite, developing from eggs, find their way into the body of their host. It was until recently considered a proof of the doctrine of spontaneous generation that, after a time, animal and plant life (unicellular organisms, infusorian animalcules, etc.) appears in water supposed to contain no living thing whatever; further, that organic fluids became foul by the development of the lowest of the plants, the bacteria. At present we know that in all these cases germs of organisms, carried about by the air, are the cause of the new development of life. If the germs be killed by heating the glass and boiling the fluid, and if by suitable means the entrance of new germs be prevented, then such a 'sterilized fluid' remains permanently unchanged. It has been found, indeed, that spores, particularly of bacteria, have an extreme power of resistance, and in many cases must be boiled more than ten minutes before they are destroyed. As the final result of all the recent experiments and observations it can only be said that the *present existence of spontaneous generation is not proved.* Now the question is, With what right can one conclude that spontaneous generation neither occurs nor has ever occurred?

First Origin of Life.—Whoever, in agreement with the teachings of astronomy, adopts the view that our earth was at one time in a molten condition and has gradually cooled, must assume that life on the earth has not existed from eternity, but at some time has had its beginning. If he wish to base his explanation, not upon a supernatural act of creation, nor upon hypotheses, like that of the transference of living germs from other worlds through the agency of meteors, there is left only the hypothesis that, according to the generally prevailing and still to be observed laws of chemical affinity, compounds of carbon, oxygen, hydrogen, nitrogen, and sulphur have been brought together to produce living substance. This process is called *spontaneous generation.* If the carbon, oxygen, nitrogen, etc., which are now combined in a stable manner in organisms were formerly unstable, the conditions for the origin of organic compounds, through whose wider combination life would be possible, may have been more favorable. *Thus the hypothesis of the first origin of life through spontaneous generation is carried to a logical postulate.*

But the postulate cannot be extended to affirm that spontaneous generation must even now exist. Since there are neither observations nor convincing theoretical considerations for such a view, there is no necessity to discuss the objections here.

II. Generation by Parents, or Tocogony.

As mentioned above, we shall deal here only with those methods of reproduction which have actually been observed, i.e., generation by parents. These methods fall mainly into two great groups, asexual and sexual generation, *monogony* and *amphigony,* to which may be added a third group, a combination of these two methods of reproduction.

a. Asexual Reproduction. Monogony.

Monogony Defined.—The chief characteristic of asexual reproduction is the fact that for it only a single organism is necessary. But since, in certain modes of sexual reproduction (hermaphroditism, parthenogenesis), this also holds true, further explanation is necessary. Asexual reproduction must be a result of the growth of the organism. This growth may be general and result in an equal growth of all parts; or it may be local and consequently lead to the formation of an outgrowth in the region of greatest increase. In the first case division takes place, in the latter budding.

Division.—In the case of division (*cf.* figs. 119, 122, 145) an animal separates into two or more equivalent parts, so that it is not possible to distinguish the mother and the daughter animal; for the original animal has completely disappeared in the young generation. The division is commonly a transverse one, in which the plane of division stands perpendicular to the long axis of the animal; less common is longitudinal division, rarest is oblique division (the planes of division passing in the direction of the long axis, or forming an acute angle with it).

Budding.—In the case of budding, the products are unequal. One animal maintains the identity of the mother animal; on the contrary, the bud, the outgrowth caused by local increase, appears as a new formation, as the daughter individual. Yet the difference between division and budding is bridged by intermediate conditions; for, if we start with binary division, this will approach budding in the same degree as the division products become unlike, so that the one takes on more and more the character of a bud, the other retaining the character of the mother organism. Such transitions are chiefly possible in the case of *terminal budding*, where the buds appear at one end of the main axis of the maternal organism. The character of budding is, on the contrary, unmistakable if the buds arise as lateral outgrowths of the mother

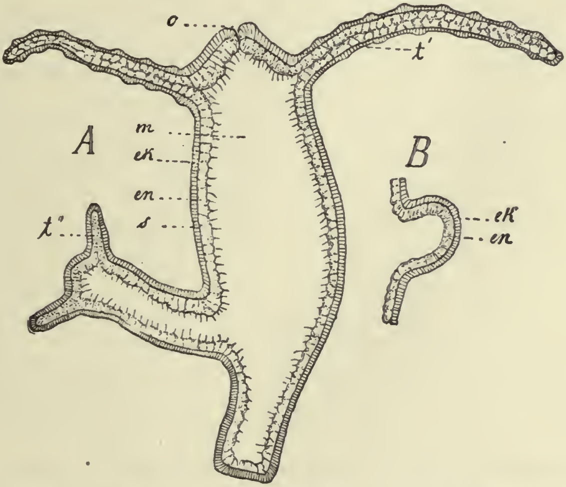


FIG. 90.—*A*, *Hydra grisea* in optical section with a bud; also *B*, first stage of a bud. *en*, entoderm; *ek*, ectoderm; *s*, supporting lamella; *t′*, tentacle of the mother animal; *t″*, tentacle of the bud; *m*, stomach; *o*, mouth.

(fig. 90), or if from the same mother numerous buds are simultaneously cut off (lateral and multiple budding) (compare fig. 20).

b. Sexual Reproduction: Amphigony.

Amphigony Defined.—For sexual reproduction two animals are commonly necessary, a female and a male; the reproductive cells—the eggs—of one must be fertilized by the reproductive cells—the spermatozoa—of the other, and thus acquire the capacity of giving rise to a new organism. Now, since there are hermaphroditic animals which produce simultaneously eggs and spermatozoa, and since with many of them at least the possibility of self-fertilization has been demonstrated, it becomes clear that the emphasis in the definition of sexual reproduction must be laid, not upon the individual, but upon the sexual products. Consequently the essential point of sexual reproduction is to be sought in the union of male and female sexual cells.

Parthenogenesis and Pædogenesis.—This explanation is applicable to by far the greater majority of cases, namely, to all cases where the term sexual reproduction can be applied. Still, in the course of the last thirty years it has been demonstrated in many instances that two modes of reproduction formerly considered as monogony, parthenogenesis and pædogenesis, must be regarded as special modifications of sexual reproduction, although the above-mentioned conditions are not strictly satisfied. In both cases the eggs develop on account of some peculiar internal stimulus, *without the occurrence of fertilization by spermatozoa.* In case of *pædogenesis* there is the additional circumstance that reproduction is accomplished by animals which have not completed their normal development; for example, the larvæ of certain flies reproduce before they have passed through the pupal stage and become flies. Pædogenesis consequently is parthenogenesis in an immature organism.

Parthenogenesis and Typical Amphigony.—Some have attempted to exclude parthenogenesis from sexual reproduction by claiming that those eggs which develop parthenogenetically are pseudova, structures which are not actual eggs. This view is absolutely untenable in view of the proof that the 'pseudova' arise just like ordinary eggs and develop like them, since they cleave and form germ-layers. The equivalence of parthenogenetic eggs to those which are fertilized is best shown in the case of the bee, where similar cells give rise to a female or a male insect according as they are or are not furnished by the queen during oviposition with a spermatozoon. Parthenogenesis is, therefore, not an asexual reproduction which was antecedent to sexual reproduction, but rather a reproduction which must have been derived from the sexual; it is *a sexual reproduction in which a degeneration of fertilization has taken place.* Such facts show that, for the essential point of sexual reproduction, fertilization (the entrance of the spermatozoon) forms indeed an extremely important, but a by no means indispensable, characteristic. To all cases comprised under amphigony this definition alone applies: *sexual reproduction is a reproduction by means of sexual cells.*

Sexual and Somatic Cells.—The distinction of sexual cells from the asexual reproductive bodies, the parts arising by division and budding, is shown by their relations to the vital processes of animals. The cells of a bud have had a share in the vital processes of the animal before the beginning of reproduction; they were functional or 'somatic' cells. In the fresh-water polyp (fig. 90), when a bud arises, the cellular material employed is that which was previously related to the mother animal in exactly the same manner as the other parts of the body wall. The sexual cells of an animal, on the contrary, are permanently, or at least for a long time, excluded from the vital processes, remaining in a resting condition, and conserving their vital energies. Therefore there are also lacking in sexual reproduction the relations to growth which are so remarkable in asexual reproduction. For, although very often sexual reproduction does not begin until the bodily growth is completed, yet it is found repeatedly that animals, as for example all fishes, continue to grow after the beginning of sexual maturity, until they are double or many times their size at that time. Sexual reproduction is not even a special form of growth, but a complete renewal of the organism, a rejuvenescence of it. This explains the important fact that asexual reproduction is most common in the lower animals (cœlenterates, worms), but is lacking from vertebrates, molluscs, and arthropods. The higher the organization of the animal the more the vital energies of its cells must be employed to meet the increasing demands upon their functional capacity, and so the more necessary is sexual reproduction.

c. Combined Modes of Reproduction.

Occurrence in the Same Species.—Very often two modes of reproduction occur in one and the same species of animal side by side. Many corals and worms have the power of multiplying by division or budding, and also of forming eggs and spermatozoa; again, others have no asexual reproduction, but their eggs develop according to circumstances, either parthenogenetically or after fertilization. The appearance of two kinds of reproduction is very often governed by the fact that individuals with different modes of reproduction alternate in a quite definite rhythm with each other. Such a development is called *alternation of generations* in the wider sense, and of this two special forms are distinguished: metagenesis, or alternation of generations in the narrower sense (progressive alternation of generations), and heterogony (regressive alternation of generations).

Progressive Alternation of Generations. Metagenesis.—Alternation of generations in the narrower sense, or *metagenesis,* is the alternation of at least two generations, of which one reproduces only asexually, by division or budding, the other either exclusively, or at least to a great extent sexually. The first generation is called the nurse, the second the sexual animal. The reproduction of hydromedusæ furnishes the best example (fig. 91). The nurses here are the polyps, which, united with one another usually in numbers into a colony, never produce sexual *organs,* but bud sexual *animals,* the *medusæ.* The medusæ are altogether unlike the polyps, being much more highly organized, and freely motile; only very rarely have they preserved the asexual mode of reproduction; on the other hand, they develop eggs and spermatozoa, from which the non-motile nurses, the polyps, develop. This example shows

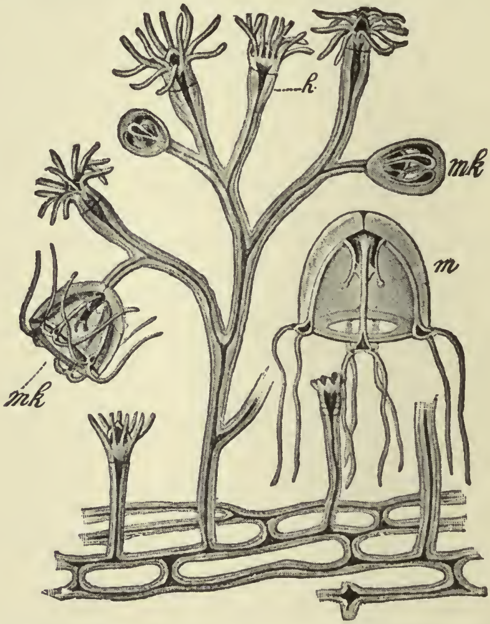


FIG. 91.—*Bougainvillea ramosa.* (From Lang.) *h*, hydranths (nurse) which have given rise to medusa-buds (*mk*); *m*, separated medusa, *Margelis ramosa* (sexual animal).

that, in alternation of generations, there is not only a difference in the mode of reproduction, but usually, in addition, a difference in form and organization. Between polyp and medusa the difference is so great that for a long time these two, though representatives of the same species, were referred to quite different classes of the animal kingdom. In many cases the alternation of generations may be still further complicated by two asexual generations following each other, before the return to the sexual generation takes place; one speaks then of grand-nurse, nurse, and sexual animal.

Heterogony is distinguished from metagenesis by the fact that the asexual generation is replaced by parthenogenesis. Consequently there alternate animals of sometimes quite different structure, of which the one arises from fertilized, the other from unfertilized, eggs. Certain Crustacea, the Daphnidæ, show heterogony in a typical manner. During a large part of the year only females are found; these increase parthenogenetically by 'summer eggs'; then males appear for a short time; they fertilize the 'winter eggs,' which now are formed, from which again parthenogenetic generations arise. Very often heterogony has been insufficiently distinguished from metagenesis, chiefly for the reason that parthenogenetic reproduction was regarded as an asexual mode, as was the case in the trematodes. The sexually ripe *Distomum* produces very peculiar *sporocysts;* these again give rise parthenogenetically to the larvæ of *Distomum,* the cercariæ. For a long time the erroneous view was held that the cells from which the cercariæ arose were not eggs, but 'internal buds,' 'germinal granules.' On the other hand there have been included under heterogony modes of reproduction in which no parthenogenesis whatever occurs. Cases have been called heterogony when two generations which have only different forms and organization alternate. *Ascaris nigrovenosa,* an hermaphroditic worm, lives in the frog's lungs; it produces the separate-sexed *Rhabdonema nigrovenosum* living in mud, from whose eggs the ascarid of the frog is again produced.

GENERAL PHENOMENA OF SEXUAL REPRODUCTION.

In sexual reproduction a series of developmental processes is observed which is repeated in an essentially similar manner in all multicellular animals, and hence these should be spoken of here together. They are: (1) the maturation of the egg; (2) the process of fertilization; (3) the process of cleavage; (4) the formation of the three germ-layers.

1. *Maturation.*

The egg with the large vesicular nucleus (germinal vesicle) cannot yet be fertilized; to render it capable of fertilization it must undergo a series of changes—the process of maturation, which consists in the replacement of the germinal vesicle by a much smaller egg-nucleus, and simultaneously the formation at one pole of the egg of the 'directive corpuscles' or 'polar bodies.'

Formation of the Polar Bodies.—The germinal vesicle initiates the changes, its walls disappearing, its contents in part mingling with the cytoplasm of the egg, in part being employed for the formation of a nuclear spindle (directive spindle). The latter places itself with its axis in a radius of the egg so that one pole is turned towards the centre, the other being in the superficial layer of the egg (fig. 92, *a*). Now begins a regular cell-division, but the products of the division are of very unequal size; the larger part is the egg, the smaller quite insignificant part is the polar body (fig. 92, *b, c*). The latter projects above the surface carrying with it one half of the spindle, and when the globule is cut off half of the spindle is included in it.

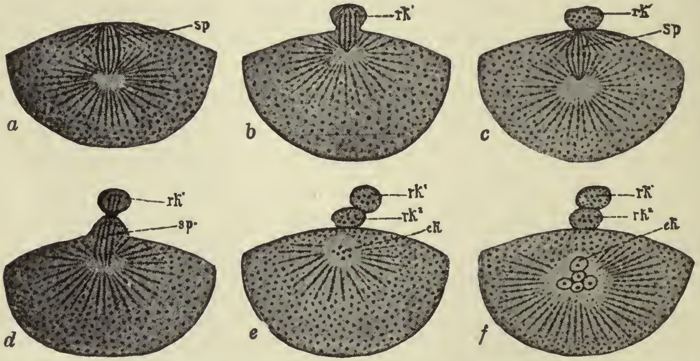


FIG. 92.—Successive stages in the formation of the polar bodies of *Asterias glacialis*. *sp*, directive spindle; rk^1, first polar body; rk^2, second polar body; *ek*, egg-nucleus in process of formation.

The Second Polar Body.—The part of the directive spindle remaining in the egg immediately forms a new spindle; the cell-budding is repeated and leads to the formation of the second polar body. As a result two small cells (fig. 92, *d, e, f*) lie at one pole of the egg, in many cases even three, since during the formation of the second polar body the first may have again divided. The part of the directive spindle still remaining after the second division becomes a vesicular resting nucleus, the *egg-nucleus*, the characteristic feature of the ripe egg capable of fertilization. In other words, by a double division there have been formed from the immature egg four (sometimes three) cells, of which one has received by far the greatest part of the original mass of the cell and constitutes the ripe egg, while the others are small bodies like rudimentary eggs. The name directive corpuscles was given to them because in very many cases their position renders possible a definite orientation of the egg; i.e., a diameter, the long axis, can be passed through the egg, one end of which is marked by the directive corpuscles. With reference to later processes of development this end is called the *animal pole* of the egg, the opposite end the *vegetative pole*.

Relation between Maturation and Fertilization.—In many cases the maturation takes place before the entrance of the sperm, either in the ovary or at the beginning of the oviduct; in many animals, on the contrary, there ensues a pause after the first polar body has been formed; the egg then requires the penetration of a spermatozoon in order to complete the further changes, i.e., the formation of the second polar body and reconstruction of the egg-nucleus. This dependence of the last phenomena of maturation upon the beginning of fertilization led for a long time to the error that the formation of the polar bodies was a part of the fertilization process itself.

2. *Fertilization.*

Copulation and Artificial Fecundation.—The term 'fertilization' in the scientific sense refers to the internal processes which, after the meeting of the egg and spermatozoon, go on in the interior of the former and end with a complete fusion of the two sexual cells; on the other hand, special expressions are necessary for those preparatory processes whose purpose is to render fertilization possible. Very often, but not in all cases, there is necessary an active transfer of the sperm from the male to the female, a *copulation*. In case of many marine animals, particularly most fishes, echinoderms, cœlenterates, the eggs and the spermatozoa are discharged into the water, and the union of these (impregnation or fecundation) depends upon chance. One can bring about then artificially what is accomplished by nature, by obtaining from the sexual organs the ripe products and bringing them together. For example, by suitable pressure upon the body of sexually ripe fishes the eggs may be collected in one dish, the sperm in another, and the contents of the latter poured over the former, and thus in many cases an entirely normal development may be obtained. Such a proceeding is called artificial impregnation.

Fertilization.—The process of fertilization in the narrower sense begins with the entrance of the spermatozoon into the egg. Usually the egg is surrounded by a gelatinous envelope, the chorion, to the surface of which the spermatozoa adhere, and through which they bore until they reach the surface of the egg (fig. 93). But since the chorion, particularly in eggs which are laid in the air, may be hard and resisting, there exists in it very often a special arrangement, the *micropylar apparatus,* rendering possible the entrance of the spermatozoon; this may be a single canal extending through the chorion, as in the eggs of fishes, or a group of such canals, as in those of almost all insects.

Monospermy and Polyspermy.—Many spermatozoa may pass through the gelatinous envelope, or through the micropyle canal, but under normal conditions only one serves for fertilization. The spermatozoon which is in the slightest degree ahead of the others is met by a process of the protoplasm by means of which it enters the egg. The egg is now impervious to all others. Only in the case of pathological eggs can two or more spermatozoa enter and then multiple impregnation (di- or polyspermy) occurs, a pathological phenomenon. There are means of protection against this abnormal fertilization. One, though by no means the only one, is the formation of the yolk-membrane, an impermeable envelope which is suddenly secreted from the surface of the egg, as soon as the spermatozoon has accomplished the impregnation. Within the yolk-membrane the body of the egg contracts into a smaller volume by discharging some of the more fluid constituents, so that between the yolk-membrane and the surface of the egg a cavity is formed easily recognized in smaller fertilized eggs (fig. 93, *B*).

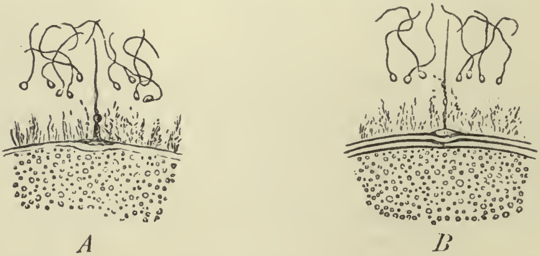


Fig. 93.—Egg of *Asterias glacialis* during fecundation. (After Fol.) *A*, entrance of the spermatozoon; *B*, the spermatozoon has entered: the yolk-membrane has formed.

In the large yolk-laden eggs of many insects and vertebrates several spermatozoa may normally enter. But this does not alter the conception of fertilization, for even here but one spermatozoon fuses with the egg-nucleus, the others degenerating sooner or later.

Essential Feature of Fertilization.—After the spermatozoon has penetrated into the egg, the head and the middle piece which contains the centrosome can still be recognized, as the chromatic and achromatic parts of the spermatozoon or sperm-nucleus (male pronucleus), while the tail and the slight amount of protoplasm disappear in the yolk. In the cytoplasm of the egg the centrosome of the sperm-nucleus gives rise to conspicuous rays, like those observed during division. Preceded by these rays the sperm-nucleus travels towards the egg-nucleus until it reaches (fig. 94); and fuses with it to form a single cleavage nucleus. Now the centrosome divides into two, which migrate to opposite poles of the nucleus, while the cleavage nucleus changes to a cleavage spindle, which divides and thus initiates the embryonic development, the successive divisions being known as the cleavage or segmentation of the egg. Since not until this point is fertilization complete, we arrive at the fundamentally important proposition that the *essential feature of fertilization consists in the union of egg and sperm nuclei.*

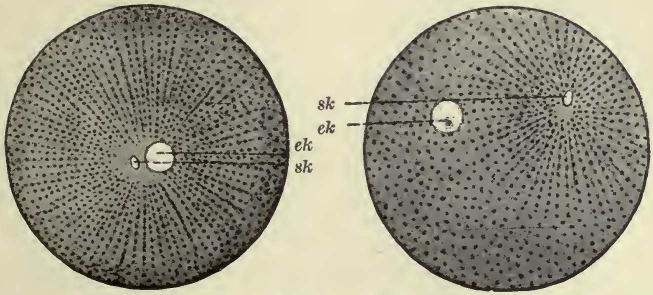


FIG. 94.—Stages in the fertilization of the egg of the sea-urchin. (After O. Hertwig.) The sperm-nucleus (*sk*) with its rays is near the surface in one egg, in the other near the egg-nucleus (*ek*).

Part Played by the Two Nuclei in Fertilization.—In many cases an abbreviation of development may take place, the stage of the cleavage nucleus being omitted, and the egg and sperm nuclei, without previously uniting, pass directly into the cleavage spindle. This fact in no wise alters the above-mentioned proposition, but yet it is important, because it shows more plainly in what way the two nuclei participate in the formation of the cleavage spindle. It shows that of the chromosomes which form the equatorial plate of the nucleus, exactly one half are furnished by the egg-nucleus, the other by the sperm-nucleus. For, even before the spindle has been formed and the contour of the two nuclei has disappeared, the chromosomes destined for the spindle are completely developed in exactly the same number in each of these (fig. 95).

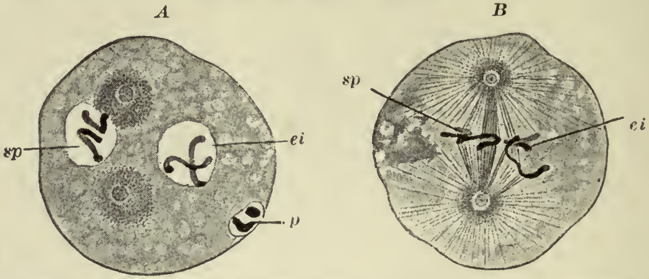


FIG. 95.—Fertilization of *Ascaris megalocephala*. (After Boveri.) *A*, the ends (centrosomes) of the spindle formed; *B*, the spindle completed; *sp*, sperm-nucleus with its chromosomes; *ei*, egg-nucleus; *p*, polar bodies.

Heredity.—Recent observations have furnished a certain basis for the doctrine of heredity. By heredity we understand the transmission of parental characteristics to the offspring. This transmission, on the whole, takes place with equal energy from the father's and from the mother's side; if we take the average of numerous cases, the result is that the child's peculiarities hold the mean between the peculiarities of father and mother; or, in other words, male and female individuals in the average have an equal power of transmitting characteristics.

The Physical Basis of Heredity.—Since in case of all animals with external fertilization a material connexion between parents and offspring can exist only through the sexual cells, these latter must contain the substances which render heredity possible; further, the two hereditary substances, in cases of equal capacity for transmission, must be present in the egg and in the spermatozoon in equal quantity. By this course of reasoning, the chromatic nuclear substance which forms the chromosomes has come to be regarded as the bearer of heredity; for we know that the egg contains a great quantity of cytoplasm, but the spermatozoon only the slightest trace of it; that, on the other hand, egg-nucleus and sperm-nucleus furnish equivalent substances, and particularly the same quantity of chromosomes, to the cleavage spindles; hence only the chromatin can be regarded as the hereditary substance (idioplasm). This supports the view expressed before (p. 67) that the nucleus is the bearer of hereditary qualities and determines the character of the cell.

3. *Cleavage Process.*

Arrangement of the Cleavage Planes.—The fertilized egg-cell divides in rapid succession into 2, 4, 8, 16, etc., cells, which become continually smaller, since the mass of the egg does not increase. The cells are called cleavage spheres, or blastomeres, the whole process the cleavage process, or segmentation, because, at each division, furrows arise on the surface which continue to penetrate more deeply (fig. 93). As a rule each new plane of cleavage is as nearly as possible perpendicular to the preceding. Hence the first three cleavage planes, which cause the division into 2, 4, and 8 parts, are similarly arranged in almost all animals. Using the globe as a basis for comparison, one speaks of a first and a second meridional furrow (I, II), and calls the third the equatorial furrow (III). The intersections of the two meridional furrows form the poles of the egg, the *animal* and the *vegetative*, so called because the material of the one is used chiefly for animal organs (nervous system), the material of the other for vegetative organs (digestive tract).

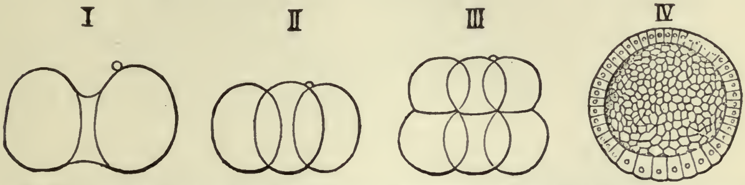


Fig. 96.—The equal cleavage of *Amphioxus lanceolatus.* (After Hatschek.) I, division into two (formation of the first meridional furrow); II, division into four (second meridional furrow) forming four cleavage spheres (fourth is hidden); III, division into eight (equatorial furrow; the seventh and eighth cleavage spheres hidden); IV, blastula in optical section. A single layer of cells surrounds the cleavage cavity. In I, II, III, a polar body is shown.

Influence of the Yolk upon Segmentation.—Different kinds of cleavage processes are distinguished, the peculiarities of which depend upon two factors: (1) upon the quantity of material, food-yolk, serving for nourishment of the egg; (2) upon the arrangement of this. The food-yolk hinders the division, since it is a material which is incapable of active movement, and is only passively divided through the activity of the protoplasm in the cleavage cells. The more the mass of this increases in proportion to the protoplasm, the more slowly does the cleavage process proceed. Finally there comes a point where the resistance of the yolk becomes so great that the protoplasm is no longer able to carry out the work completely; then only the protoplasmic part of the egg is divided, that which is rich in yolk remaining an undivided mass. In this case one speaks of a *partial* cleavage in comparison with the ordinary and more primitive mode, the *total* cleavage; further, the eggs which show a partial cleavage are called *meroblastic*, because only the segmented part of the egg is directly employed in the formation of the embryo or bud (βλαστός), while the undivided main mass serves merely as food-material in the course of growth. Eggs with total cleavage, on the contrary, are called *holoblastic*.

Distribution of the Yolk.—The arrangement of the yolk is connected with the position of the nucleus; either the egg-nucleus maintains a central position and collects the yolk concentrically around itself (*centrolecithal eggs*) (fig. 97), or it is pushed, together with the greater part of the protoplasm, to one pole of the egg, while at the other pole the yolk predominates (*telolecithal eggs*). Since the nuclear pole, in the course of development, always becomes the animal pole, there can be distinguished in the egg an animal part rich in protoplasm and a vegetative part rich in yolk (fig. 98). In many telolecithal eggs the two regions pass gradually into one another, but in others a distinct boundary separates an almost purely protoplasmic animal portion from a yolk-containing vegetative portion. This condition is well shown in the bird's egg (fig. 99). Here only the yolk is to be regarded as an egg in the embryological sense, while the white, the egg-membrane, and the calcareous shell are only later depositions upon the surface of the egg. The chief mass of the yolk is deutoplasm, upon which rests a thin layer of protoplasm, the germinal disc, always uppermost

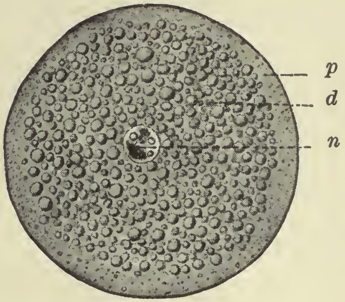


FIG. 97.

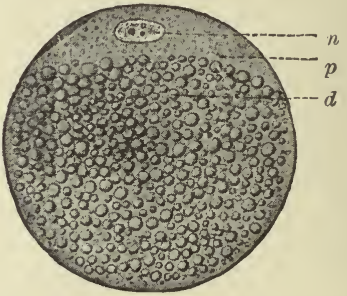


FIG. 98.

FIG. 97.—Centrolecithal egg. (After O. Hertwig.) *n*, nucleus; *p*, portion of the egg rich in protoplasm; *d*, portion rich in yolk.

FIG. 98.—Telolecithal egg. (After O. Hertwig.) Letters as in fig. 97.

whatever the position of the egg. The protoplasmic layer contains the egg-nucleus, and, after fertilization, by progressive development continually separates itself (blastoderm) more and more sharply from the underlying yolk.

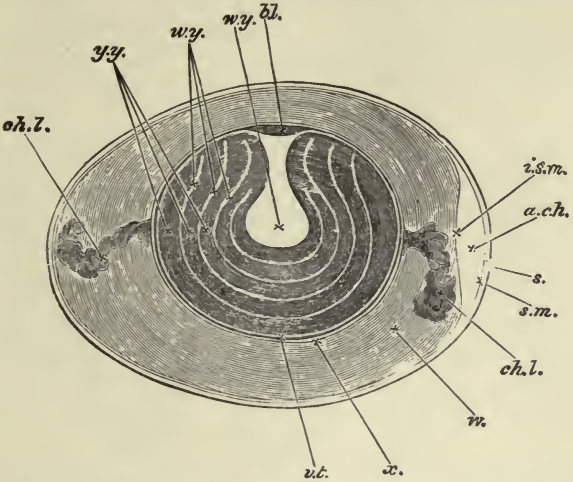


FIG. 99.—Diagrammatic longitudinal section through a bird's egg. (After Balfour.) (1) The egg: *b.l.*, blastoderm; *w.y.*, white yolk: *y y.*, yellow yolk. (2) Coverings of the egg: *v.t.*, yolk membrane (vitelline membrane); *x.* and *w.*, inner and outer layers of white; *ch.l.*, chalazæ; *i.s.m.* and *s.m.*, inner and outer shell-membrane; between them at the right end is the air-chamber (*a.c.h.*); *s*, shell.

Various Types of Cleavage.—After the foregoing remarks a brief explanation will suffice to render intelligible the following figures of the various modes of cleavage.

a. Holoblastic Eggs with Total Cleavage.

1. *Equal Cleavage.*—The yolk, present only in small quantity, is distributed equally through the egg; upon cleaving, the egg divides into parts of approximately the same size and equally rich in yolk (alecithal eggs, fig. 96).

2. *Unequal Cleavage.*—The yolk is abundant, but not in such a quantity as to prevent complete cleavage; it lies especially at the vegetative pole of the egg, causing the cleavage in this region to progress more slowly; here larger cleavage spheres are formed, because richer in yolk; hence the embryo, at the very first, is found to be composed of smaller animal cells poor in yolk, and larger vegetative cells rich in yolk (telolecithal, holoblastic eggs, figs. 100 and 101). In some instances of unequal cleavage the

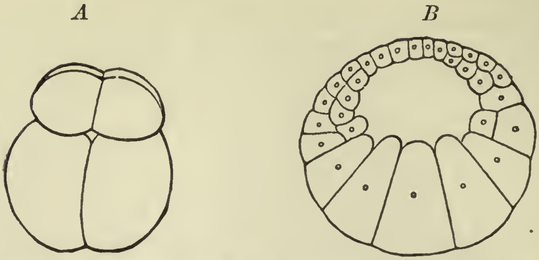


Fig. 100.—Unequal cleavage of the egg of *Petromyzon*. (After Shipley, from Hatschek.) *A*, stage of eight cleavage spheres; *B*, blastula in meridional section. The dissimilarity of the cleavage spheres begins with the equatorial furrow.

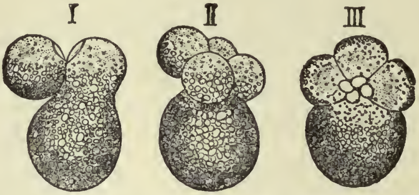


Fig. 101.—Unequal cleavage of a snail's egg, *Nassa mutabilis*. (After Bobretzky.) I, the first meridional furrow has divided the egg into unequal parts; II, the second meridional furrow has formed three smaller and one larger cleavage sphere (seen from the side); III, the equatorial furrow has formed four smaller animal and four larger but unequal vegetative cells (seen from the animal pole).

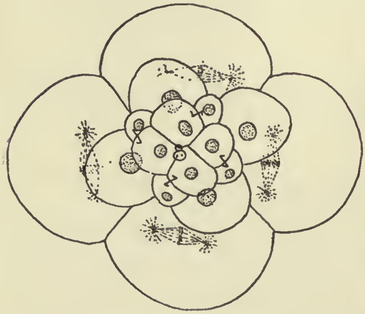


Fig. 102.—Spiral cleavage in *Crepidula*. (After Conklin.)

cells are in straight lines (fig. 100, *A*), but in others the cells alternate (fig. 102); this is called spiral cleavage and is common in several groups.

b. Meroblastic Eggs with Partial Cleavage.

3. *Discoidal Cleavage.*—The yolk is so collected in the vegetative portion of the egg that it prevents cleavage; cleavage, therefore, is limited to the region around the animal pole and here forms a disc of small cells, the anlage of the embryo, or *blastoderm* (telolecithal, meroblastic eggs) (figs. 99, 103).

4. *Superficial Cleavage.*—The yolk is collected in the centre of the egg and prevents cleavage; in consequence of this only the outer layer of the egg divides into cells, which, in the form of a continuous superficial layer, enclose the unsegmented central mass (centrolecithal eggs) (fig. 104).

Distribution of the Types of Cleavage.—Of the four types of cleavage mentioned the superficial one has an interest from the point of view of the systematist, since it occurs exclusively in the arthropods. The other modes of cleavage are distributed as follows: the discoidal has been observed in the majority of the vertebrates and in the most highly organized molluscs, the cuttlefishes, while the equal and the unequal cleavage can be found in all the groups of the Metazoa.

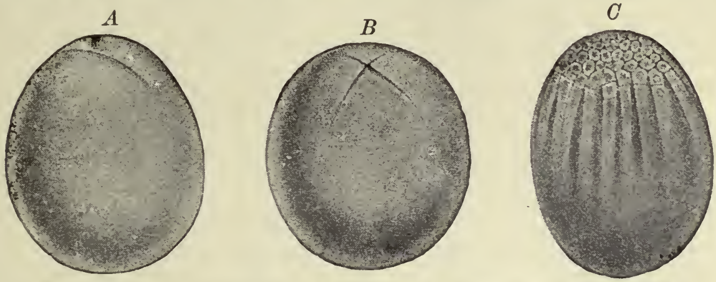


FIG. 103.—Discoidal cleavage of the egg of a cephalopod (*Loligo pealii*). (After Watase.)

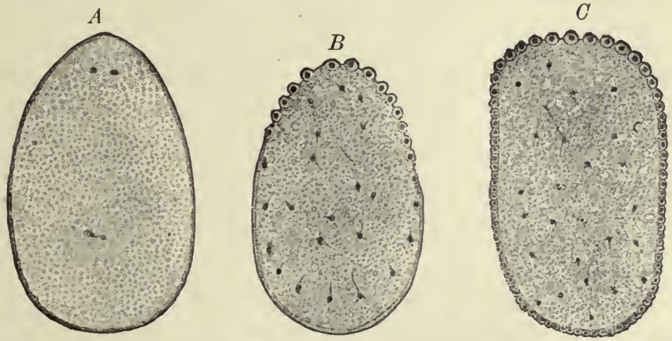


FIG. 104.—Superficial cleavage of an insect egg (*Pieris cratægi*). (After Bobretzky.) *A*, division of the cleavage nucleus; *B*, movement of the nuclei to the periphery to form the blastoderm; *C*, formation of the blastoderm.

Blastula.—Sometimes during the first stages of segmentation, sometimes later, there is usually formed a cavity, the *cleavage* or *segmentation cavity*, between the cells in the interior of the egg; with the progress of development this cavity becomes continually larger (fig. 100, *B*). Around it the cells lie in the form of a one-layered or of a many-layered epithelium and form the blastoderm; hence the name for this stage, *blastodermic vesicle*, or, briefly, *blastula*. The more yolk there is present, the smaller is the cleavage cavity; in centrolecithal eggs with superficial cleavage it is entirely absent.

4. *Formation of the Germ-layers.*

Gastrula.—Besides the blastula there is still a second stage of development, the gastrula or the two-layered embryo, which is common to all the Metazoa. This stage is understood easiest in the case of eggs which have an equal cleavage (fig. 105, *B*); here it has the form of a double-walled cup with a wider or narrower mouth. The cavity of the cup (the primitive digestive tract or *archenteron*) is the beginning of the most important part of the digestive system; the opening is the primitive mouth or *blastopore* (*prostoma*). Of the two layers of cells forming the wall of the cup and uniting at the blastopore, the external is the *ectoderm* or outer germ-layer, the internal the *entoderm* or inner germ-layer. In the gastrula we meet for the first time the formation of germ-layers, i.e., the formation of definite embryonic layers marked off from each other, the cells not yet differentiated, from which organs arise through organological and histological differentiation.

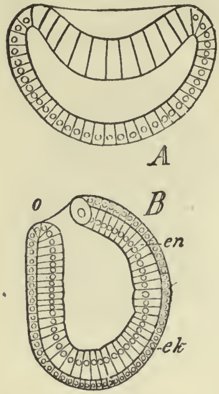


FIG. 105.—Gastrulation of *Amphioxus*. (After Hatschek) The animal pole here is above, and the vegetative pole below, in comparison with fig. 93. In fig. *A* the cells of the vegetative pole are beginning to sink in; *B*, the invagination completed, the cleavage cavity reduced to a slit between the entoderm (*en*) and the ectoderm (*ek*); *o*, blastopore.

Invagination.—The gastrula is formed from the blastula by *invagination* (fig. 105, *A*). The result is the same as when by pressure of the finger upon a hollow india-rubber ball one side is pressed in against the other; the layer of vegetative cells gradually sinks in and becomes surrounded by the cells of the animal pole (fig. 105, *B*). Thus there arises in the egg, in addition to the cleavage cavity, a new cavity, the anlage of the lumen of the digestive tract; this increases and finally obliterates the cleavage cavity, so that the invaginated part of the blastoderm, the entoderm, becomes pressed against the part which remains external, the ectoderm.

Modified Modes of Gastrulation.—In the case of eggs with much food-yolk the relation of the structure and of the mode of formation of the gastrula is more difficult to understand. Here, however, it is sufficient to mention the fact that the gastrula stage has fortunately been discovered for almost all eggs with a great quantity of food-yolk, and that the yolk-material finds lodgment principally in the entodermal cells.

Epiblast and Hypoblast.—For outer and inner germ-layer the terms epiblast and hypoblast, upper and lower germ-layer, have been much used; these names are strictly applicable only to those eggs with discoidal cleavage. In the bird's egg, for example, the two germ-layers form over the unsegmented yolk, from which they become separated by the gastrular cavity; thus, then, the external germ-layer actually lies above, the internal below. Other terms for the two germ-layers are entoblast and ectoblast.

Delamination.—In regard to the mode of development of the gastrula many controversies have arisen which are not yet finally settled; in addition to invagination there may exist a second, but very much less frequently occurring mode of development, delamination. In delamination the blastula may become two-layered by tangential division of its cells (fig. 106); each single blastoderm-cell, or, at least, the majority of these cells, by this division falls into a peripheral ectodermic and a central entodermic cell. In case of delamination the cleavage cavity becomes directly the cavity of the digestive track, a fact which renders it difficult to regard delamination and invagination as modifications of one and the same process.

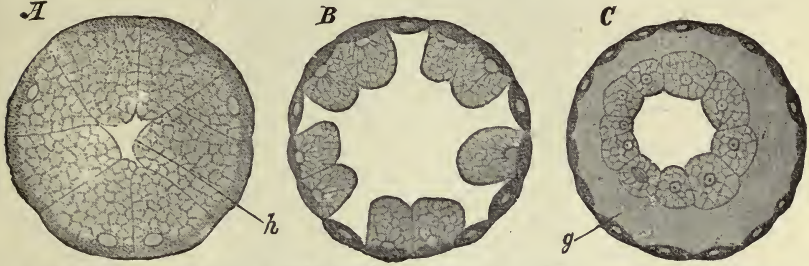


FIG. 106.—Delamination of the egg of a Geryonid. (After Fol, from Korschelt-Heider.) *h*, cleavage cavity; *g*, jelly.

Formation of the Mesoderm. The Mesenchyme.—Many lower animals, e.g. most cœlenterates, have in general only two germ-layers. When these are laid down there begins immediately the differentiation of muscle and nerve fibres and the other processes of histological changes of the cells, as well as a series of changes of form, by which the gastrula becomes the adult animal. In higher organisms, on the other hand, before further differentiation begins, there arises still a third germ-layer, which, owing to its position between the first two, is called the mesoderm, mesoblast, or middle germ-layer; this naturally can come only from the cell material of the existing germ-layers, and indeed only the entoderm seems to participate in it. Two methods can be distinguished in its formation. In one the space between ectoderm and entoderm becomes widened by the secretion of gelatinous substance, and from the entoderm isolated cells push into this jelly; thus there arises a middle layer, the *mesenchyme* (fig. 107), somewhat similar to gelatinous connective tissue, from which certain organs either wholly or in part take their origin.

Mesothelium.—In the second case the mesoderm may preserve the epithelial character of the two primary germ-layers, so that it is called *mesothelium*. The mesothelium is cut off from the entoderm, the mode of development being shown in the embryology of the worm *Sagitta* (fig. 108).

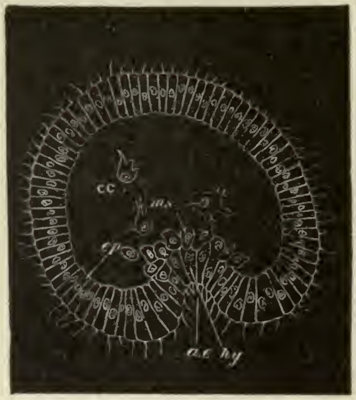


FIG. 107.—Formation of the mesenchyme and beginning of gastrulation in *Holothuria tubulosa*. (After Selenka, from Balfour.) *cc*, cleavage cavity; *ep*, ectoderm; *hy*, entoderm; *ms*, mesenchyme cells; *ae*, archenteron.

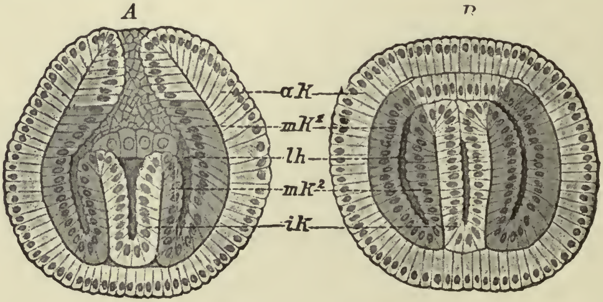


FIG. 108.—Formation of the mesothelium and cœlom of *Sagitta*. *A*. From the bottom of the gastrula arise two folds, which divide the archenteron into the permanent digestive tract and the cœlomic diverticula. *B*. The separation is almost completed by the pushing up of the folds. *ak*, outer, *mk*, middle, *ik*, inner germ-layer; *mk*¹, somatic layer; *mk*², splanchnic layer; *lh*, body-cavity.

Cœlomic Pouches.—When the gastrula of *Sagitta* has been formed two folds arise from the archenteric walls opposite the blastopore (*A*), thus partially separating a pair of lateral chambers from the rest. The process continues; the blastopore closes, while the entodermal folds extend to the opposite side, where they fuse with the walls (*B*). In this way a pair of cœlomic pouches are cut off from the rest of the archenteron which forms the lumen of the digestive tract and its derivatives, while the walls of the pouches form the mesothelium, that of the digestive region the secondary entoderm. In each cœlomic pouch two walls are recognizable, an inner or splanchnic layer which unites with the entoderm to form the wall of the digestive tract, the *splanchnopleure,* while the somatic layer unites similarly with ectoderm to form an outer body wall, the *somatopleure.* From the foregoing it is evident that the mesothelium is strictly not a single layer, but consists of two layers which pass into each other, and that its origin is closely connected with the formation of the body cavity.

Occurrence of Mesenchyme and Mesothelium.—There are three possible methods for the distribution of mesenchyme and mesothelium, and these actually occur. There are purely mesenchymatous animals, like the flat-worms, and purely mesothelial, like *Sagitta,* many annelids, and *Amphioxus;* but there are also animals in which the mesoderm consists of mesenchyme and mesothelium: either the mesenchyme arises first and later the mesothelium, as in the echinoderms, or the reverse order is followed, as in most vertebrates.

Histological and Organological Differentiation.—All the organs of an animal arise from the three germ-layers in this way: first, embryonic cell material is marked off into separate complexes, usually by infolding (*organological differentiation*), and then later these become changed into tissues (*histological differentiation*). The details differ in the various animal groups; the following is the most general: from the *ectoderm* arise the skin with its glands and appendages, the nervous system, and the sensory epithelium; the *entoderm* gives rise to the most important part of the digestive tract with its glands; while muscles, blood, supporting and connective substances, excretory organs, in whole or in part, arise in the *mesoderm;* the sexual organs are also usually mesodermal.

Relations of the Germ-layers in Budding.—Of late the question has often been raised as to how far the germ-layer theory is applicable to the occurrences in asexual reproduction. At first one would expect in budding, and still more in the case of division, that each organ of the daughter animal would arise from the corresponding organ of the maternal animal, or, if that be impossible by conditions of space, from a mass of tissue belonging to one of the same germ-layers. In many instances this is certainly the case, as, for example, in the budding of hydroids the entoderm and ectoderm of the bud arise from the corresponding layers of the maternal body (fig. 90). But through recent investigations exceptions to this rule have become known. In polyzoans and tunicates there are undifferentiated cells which are employed in cases of budding; these are elements without the characteristics of a definite body layer which, independently of the position they assume in the maternal animal, can be employed, according to need, in the building up of organs. In the regeneration of lost parts investigations show that it is not necessary that the missing structure, in worms and even in vertebrates, should be re-formed by the same layer from which it originally arose. The lens of *Triton* arises ontogenetically from the epithelium of the skin. If extirpated, it is regenerated from the pigmented epithelium of the iris.

5. *The Different Forms of Sexual Development.*

Embryonic and Postembryonic Development. — While the occurrences described (fertilization and cleavage of the egg, formation of the germ-layers) are going on the young animals are usually enclosed within a firm protective covering, or even in the maternal sexual apparatus (uterus), and are hence called *embryos*. Later stages, even the formation of the most important organs, may occur during embryonic life, as we see in case of the mammals, birds, reptiles, many fishes, worms, and crabs, which, at the end of their embryonic existence, are complete in all their parts, and need only the maturity of the sexual organs, and growth of the body as a whole, in order to reach the climax of their development. On the other hand, there are animals, chiefly aquatic, which, after leaving the egg, undergo important changes, like the cœlenterates, echinoderms, insects, amphibians, etc. The cœlenterates, echinoderms, and many worms usually escape from the egg even before the formation of the germ-layers, and, as free-swimming ciliated 'planulæ,' form the germ-layers and organs. Since there is here a more or less extensive post-embryonic development, it is a misnomer to apply the term 'embryology' to both stages; it is necessary, rather, to limit the name to the developmental processes inside the egg, and, on the other hand, to speak generally of the history of the development of the individual, or *ontogeny*. As the undeveloped animal within its membrane is called an *embryo*, so the name *larva* is applicable to the free-living but not completely matured animal.

Direct and Indirect Development—Metamorphosis.—Larval development may be either *direct* or *indirect*. In direct development, as the term implies, the larva pursues the direct way towards the sexually mature animal, the lacking organs being outlined one after another; hence it is continually becoming more like the sexually mature animal. In indirect development, on the contrary, organs belonging only to the larval life, and hence called *larval organs,* are formed and later are destroyed. Therefore in the definition of indirect development, or as it is commonly called *metamorphosis,* special emphasis is laid upon the presence of larval organs. Thus the caterpillars of butterflies are distinguished not only by the absence of compound eyes and wings, but also by the presence of anal feet and spinning-glands, which are absent in the butterfly, and further by the different shape of the jaws, antennæ, and legs, the different arrangement of the tracheæ and nervous system, etc. Tadpoles are distinguished from frogs not only by the absence of lungs and extremities, but also by the presence of gills and tail. The more numerous the larval organs, the more pronounced, therefore, will be the metamorphosis.

Oviparous and Viviparous Animals.—The time at which the egg leaves the mother's body is independent of that at which the embryo escapes from the egg membranes. Two extremes are known, the oviparous or egg-laying animals, and the viviparous or those which give birth to living young. Only those forms can be considered as strictly *oviparous* in which the egg at the time of laying is a single cell, in which case it is either not fertilized until after extrusion, as in the case of most fishes, sea-urchins, etc., or during extrusion, as in batrachians and insects. In *viviparous* animals, on the contrary, birth and the rupture of the egg membranes occur quite, or almost, at the same time, and from the mother there emerges an animal which has completed its development or, at least, has progressed so far that it is able to live without protective coverings.

Ovo-viviparous Animals.—Varying degrees of *ovo-viviparous* development connect these two extremes. What here appears at birth at first impresses us, on account of its covering, as being an egg; but the first stages of development have already passed, so that, by artificial rupture of the egg membranes, an embryo more or less developed, but usually not yet capable of independent life, is exposed. Birds really belong in the category of ovo-viviparous animals, for their eggs are fertilized some time before they are laid, and have already completed the formation of the blastoderm. In the case of many worms the egg-shell may contain, even at the time of laying, an animal all ready for hatching.

No Sharp Line between Oviparous and Viviparous.—Transitional forms of this kind show that no sharp line can be drawn between 'egg-laying' and 'bearing living young' and one must guard against attributing too much importance to the apparent distinctions. Linnæus, following the example of Aristotle, was in error in regarding the time of birth as of systematic importance. In many divisions of animals oviparous as well as viviparous forms are found. The majority of sharks are viviparous, but a few species lay eggs; on the contrary, for bony fishes the rule holds that the eggs are laid before fertilization. Exceptions are the viviparous surf perches, Embiotocidæ, of the Pacific coast and many Cyprinodonts of fresh water. Most of the Amphibia, reptiles, and insects are egg-layers, but not a few forms are viviparous. Even among the mammals, for which for a long time the 'bearing young alive' was regarded as diagnostic, it has been discovered lately that the *Echidna* and *Ornithorhynchus* lay eggs. Finally, exceptions to the rule occur in one and the same species. Adders commonly lay eggs, but under unfavorable conditions they retain them inside their body until ready to hatch.

SUMMARY OF THE FACTS OF ONTOGENY.

1. The development of an animal begins with an act of *generation;* spontaneous generation and generation by parents are to be distinguished.

2. *Spontaneous generation* (generatio æquivoca, or spontanea; abiogenesis) is the origin of living beings from lifeless matter (without pre-existing organisms).

3. The present existence of spontaneous generation is neither shown by observation, nor is it, on the whole, probable; yet spontaneous generation is a logical postulate, in order to explain the first origin of life on our globe.

4. *Generation by parents* (tocogony), derivation of an animal from an animal of the same or similar structure, can take place either by the sexual or the asexual mode.

5. Asexual generation may be either by division or by budding.

6. In case of division an organism grows regularly in all its parts, and by constriction falls into two or more equivalent new pieces.

7. According to the direction of the plane of division in reference to the long axis of the animal we speak of longitudinal, transverse, and oblique division.

8. In case of *budding* a local growth occurs; the local outgrowth, the bud, separates from the mother as a smaller, usually incompletely formed, animal.

9. According to the position and number of the buds we distinguish lateral, terminal, and multiple budding.

10. *Sexual reproduction* is reproduction by means of special sexual cells, which do not take part in the ordinary functions of the body.

11. In sexual reproduction two kinds of cells unite, the female egg and the male spermatozoon (fertilization).

12. In rare cases the egg develops without fertilization: *parthenogenesis;* this is a sexual reproduction with degenerated fertilization.

13. *Pædogenesis* is parthenogenetic reproduction by a young (i.e., incompletely developed) animal.

14. Different modes of reproduction (asexual, sexual, parthenogenesis, pædogenesis) may occur in the same species; then these often occur in a regular order, and in such a way that individuals with different modes of reproduction alternate with one another: *alternation of generations* in the wider sense.

15. *Alternation of generations* in the strict sense (progressive generation, *metagenesis*) is the alternation of two generations, of which one reproduces by division or budding, the other sexually. The former is called the nurse, the latter the sexual animal.

16. The alternation of parthenogenesis or pædogenesis with pronounced sexual reproduction is called regressive alternation of generations, or *heterogony.*

17. Development which is inaugurated by sexual reproduction shows in nearly all multicellular animals a general agreement in the incipient stages: fertilization, cleavage, formation of germ-layers.

18. The essential point of fertilization lies in the complete fusion of egg and spermatozoon, particularly in the fusion of the nuclei, egg and sperm nuclei, to form the cleavage nucleus.

19. *The cleavage of the egg* is a cell division, a division of the fertilized egg into the cleavage spheres (blastomeres). The cleavage may be *total* (holoblastic egg) or *partial* (meroblastic egg); total cleavage is either *equal* or *unequal,* the partial either *discoidal* or *superficial.*

20. By progressive division of the cleavage spheres, and by the formation of a cleavage cavity, there arises a one-layered embryo, the *blastula* (vesicula blastodermica).

21. By the invagination of the blastula the *gastrula* or two-layered embryo arises.

22. The gastrula contains a cavity, the primitive digestive tract or *archenteron,* opening to the exterior through the blastopore; it consists of two epithelial layers, the *entoderm* (hypoblast) or the inner germ-layer, lining the archenteron, and the *ectoderm* (epiblast) or outer germ-layer.

23. Between the inner and the outer germ-layer still a third, the middle germ-layer, *mesoderm,* may be formed.

24. The middle germ-layer arises either by an infolding or

a cutting off of a part of the entodermal epithelium, epithelial mesoderm, *mesothelium;* or by the migration of separate cells to form a gelatinous tissue (*mesenchyme*).

25. Many animals deposit their eggs before or shortly after fertilization (*oviparous*); others lay eggs which have already been fertilized in the maternal body, and at the time of laying have passed through some of the stages of development (*ovo-viviparous*). A third series of animals give birth to living young (*viviparous*).

26. The development of an animal is either direct or indirect (metamorphosis).

27. Indirect development or *metamorphosis* is where the young animal, as it comes from the egg, differs from the sexually mature animal in two points:

(*a*) by the lack of certain organs which occur in the sexually mature animals;

(*b*) by the appearance of organs, larval organs, which are lacking in the sexually mature animals.

III. RELATION OF ANIMALS TO ONE ANOTHER.

General Relations.—Just as between the organs of one and the same animal there exists a regular relation which is termed correlation of parts, so also the different individuals of the animal population stand in manifold and intimate reciprocal relations to one another. Darwin has shown, in a great number of instances, how the conditions of existence of many animal species are altered, if other forms appear or disappear, or undergo an extraordinary reduction or increase in number of individuals. Such reciprocal effects are usually of a more special nature and can be understood only by individual study; a few conditions are of wide occurrence and are hence suitable for a general consideration; to such belong colony and society formation, parasitism, and symbiosis.

I. Relations between Individuals of the Same Species.

Colony Formation.—Colony and society formation are conditions which exist between individuals of the same species. An *animal colony* is a union of numerous individual animals by an organic bodily connexion; the latter may arise in two ways: first, by animals, originally separate, approaching one another and partially fusing together; secondly, by individuals, formed by division and budding, remaining united with one another instead of separating. The first is extremely rare, and in the animal kingdom plays no rôle whatever.

Colony Formation by Fusion.—Many Protozoa fuse with one another and form larger bodies in which the individual animals can still be recognized. Among the multicellular animals, that of *Diplozoon paradoxum* (fig. 109) is the only case known where two animals (Diporpa), sprung from different eggs, normally unite into a double animal, which recalls certain double monsters, as, for example, the Siamese twins.

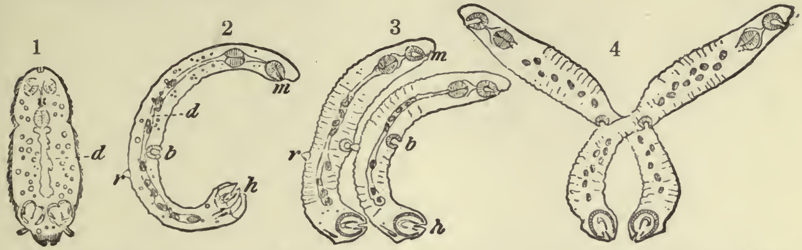


FIG. 109.—Development of *Diplozoon paradoxum*. (From Boas.) (1) Larva, from which comes (2) 'Diporpa.' (3) Two Diporpæ uniting. (4) The Diporpæ have united into *Diplozoon*. *m*, mouth; *d*, digestive tract; *h*, posterior adhering apparatus; *b*, ventral sucking-disc, which serves for attachment to the dorsal cone, *r*.

Colony Formation by Incomplete Division and Budding.—In general it can be said that the important instances of colony formation rest upon incomplete asexual reproduction. An animal forms new individuals by division or by budding, but the process is not completed since the new generation does not separate from the parent. There remain connexions of tissue uniting the buds with the mother or the sisters with each other. The colonies of marine hydroids and corals (figs. 91, 206) may consist of thousands of individuals which, by repeated incomplete budding or division, have sprung from a single sexually produced mother animal.

Community of Functions.—In the majority of cases the connexion of the tissues results in a considerable degree of community of functions. Stimuli which affect one individual are transmitted by common nerves to the others of the colony; thus movements in common are rendered possible. In a similar way the food captured and digested by one animal serves for all. On account of the community of its functions, a colony appears like a unified whole, like an individual of a higher order; the same process which led to the formation of multicellular organisms is repeated. Just as there the elementary organisms, the cells, are united into a single animal, so here the single animals are united into a colony.

Polymorphism.—When a whole is made up of numerous equivalent parts, the conditions for division of labor are present. Instead of the functions of the entire organism being distributed equally to the individual parts, many of the latter become employed solely for this, others again solely for that function, and acquire a corresponding structure. In case of such animal colonies one speaks then of multiformity or polymorphism. Polymorphism appears oftenest in connexion with the vegetative functions, leading to a distinction between sexual animals and nutritive animals, as in the case of most Hydrozoa, where often nutrition is accomplished by animals without sexual organs, and reproduction is carried on by animals without a mouth. But other functions, movement, sensation, offence and defence, may also become specialized. Siphonophores are the classical examples of polymorphism (fig. 110). Here united into a single body are locomotor

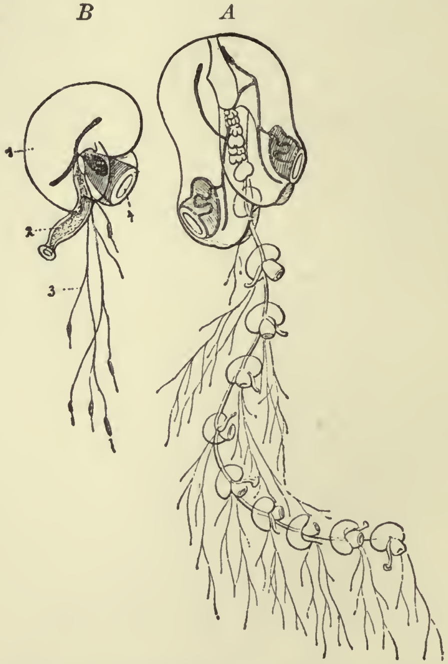


FIG. 110.—*Praya diphyes*. (After Gegenbaur) *A*, the entire animal; *B*, a single group of individuals greatly magnified (*Eudoxia*). 1, covering scale; 2, nutritive polyp; 3, nettle-threads; 4, sexual bell.

animals, the swimming-bells, serving only for locomotion; covering scales, which serve only to protect the others; nutritive polyps, which alone take in and digest food; sexual animals and tactile polyps, which are concerned only in sexual reproduction and with sensation. In regard to the other functions each animal is related to its brothers and sisters; its very existence therefore has become dependent upon these; the single individual can live only while a part of a whole. Thus also division of labor leads to greater centralization; the more polymorphic an animal colony becomes, the more unified it is, the more it gives the impression of being a single animal instead of an aggregation of single animals.

In Social Animals the reciprocal dependence of the individuals is much less, since here there exists no organic connexion, only a voluntary communal life. As asexual reproduction is of importance in the case of colonies, so here the sexual plays a prominent rôle. Under the influence of the sexual impulse, many animals, even some of the lowest organisms, flock together, either permanently or periodically; sea-urchins, sea-cucumbers, many fishes, collect near the coast at the time of egg-laying. The sexual impulse draws together herds of deer, elephants, etc. The care of the young offspring further leads to a closer organization, to a society. All insect societies are built up on this basis. Consequently, since the sexual life is the starting-point of social life, it is further comprehensible that, in the different groups of individuals forming the community, the sexual organs may be influenced in their development. Besides males and females (kings and queens) there are still other animals with degenerated sexual organs incapable of function, the workers; the latter are either only females (bees and ants) or females and males (termites). While the kings and queens give rise to the next generation, the workers care for the young, look after the hive, provide food and protection, and also serve for defence, if the latter is not delegated to a special class, the soldiers (termites).

II. RELATIONS BETWEEN INDIVIDUALS OF DIFFERENT SPECIES.

Causes of Close Relation.—Where individuals of different species stand in close reciprocal relations to each other the cause is to be found in the advantages which the one species derives from the other, or which these both furnish reciprocally; the former condition is called *parasitism*, the latter *symbiosis*.

Parasitism.—Parasites are animals which find their dwelling-place upon or in another animal, the host, and obtain nourishment from it. They have consequently come into a dependent condition and have undergone a more or less extensive change in their organization.

True Parasitism.—The fact that an animal has settled down upon another is not sufficient to characterize it as a parasite. There are many sedentary animals which, when opportunity offers, attach themselves to a stone, a plant, or another animal; in such cases the term parasitism is a misnomer, because it cannot be called a dependent condition. If a hydroid fasten itself upon the back of a crab instead of on a stone, it is the result of chance, in which the nature of the hydroid is in no way concerned. The case would be different if the polyp were able to live only upon the crab, and perished if in any other place. Such a dependent condition usually occurs only when the mode of nutrition is also dependent upon the place of abode; when the host not only serves for a dwelling-place, but also furnishes the dweller with food; when, consequently, the dweller lives at the expense of the host.

Degeneration Caused by Parasitism.—The degree to which a parasite has become dependent upon its host varies in the different species; it is determined by the extent to which the parasite has adapted itself to the organization of its host. Therefore it is necessary in speaking of parasitism to consider the changes of form which the parasitic mode of life has caused in the structure of animals. These concern most immediately the organs of locomotion and nutrition. Since a parasite needs to fix itself as firmly as possible to the host, the locomotor apparatus more or less completely disappears and an apparatus for fixation to the host becomes necessary; parasites of different groups are provided with hooks, claspers, sucking-discs, etc. The blood, tissue-fluids, or liquid food of the host furnishes nourishment to the parasite: these are substances in solution which scarcely need digestion. Usually, therefore, the digestive canal is simplified or quite disappears; among the parasites there are gutless worms as well as gutless Crustacea. The mode of life of a parasite is also simplified, since it is no longer compelled to seek its food; in all parasites the nervous system and sense-organs undergo a high degree of degeneration; the former becomes limited usually to the most indispensable portion; the latter, except those of touch, may entirely disappear.

Modification of the Sexual Apparatus by Parasitism.—The sexual apparatus, on the contrary, undergoes a strong development. While it becomes easier for the parasite to maintain itself, the existence of the species is more precarious. If a man die, then most of his parasites die with him, especially those which exist in the interior of his body. In order that a parasitic species may not become extinct in a short time, it is necessary that the eggs be introduced into a new host. Since this transmission is attended with difficulties, the parasites must produce an enormous number of eggs. The eggs, too, are distinguished by great resisting power and well-developed protective organs, such as strong shells, etc.; thus it is known, for example, that the eggs of Ascarids continue to develop for some time in alcohol, being protected by their impermeable shell.

Ectoparasites and Entoparasites.—All the above-mentioned phenomena are more conspicuous in the case of parasites which live inside of other animals, *entoparasites*, than in the case of the dwellers upon the skin or other superficial organs, the *ectoparasites*. In case of entoparasites the transforming influence of parasitism is so considerable that representatives of the most diverse animal groups take on a remarkable similarity of appearance and structure. *Pentastomum tœnioides* (fig. 112), for example, belongs in the same class with the spiders, the Arachnida, but in external appearance it is entirely unlike them, resembling the tape-worms (fig. 111). Hence for a long time all entoparasites, on account of their similarity, were united into a single systematic group under the name of 'Helminthes,' comprising members of the crustaceans, worms, and spiders, as well as animals of entirely different groups of the animal kingdom. Only by embryology was the unnaturalness of this grouping recognized. Entoparasitism therefore is one of the best examples for illustrating *convergent development*, i.e., animals of different systematic position acquiring, under similar conditions of life, a great similarity of structure and appearance.

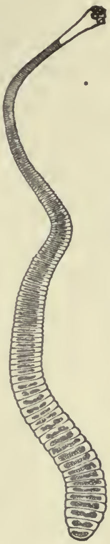


FIG. 111.

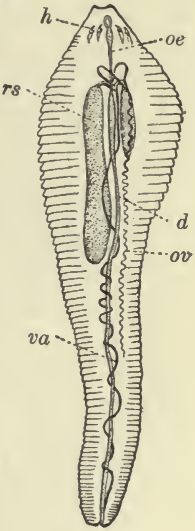


FIG. 112.

FIG. 111.—*Tœnia nana.* (After Leuckart.)

FIG. 112.—*Pentastomum tœnioides* female. (After Leuckart.) *h*, hooks right and left of mouth; *ov*, unpaired ovary, branching into two oviducts, which unite into the unpaired vagina (*va*): the latter receives the outlets of two *receptacula seminis* (*rs*), and winds around the digestive tract (*d*); *œ*, œsophagus.

Symbiosis.—Less frequent than parasitism is *symbiosis*, or the association of animals for reciprocal advantages. Social animals frequently not only hold certain animals in bondage, but even seek to protect and serve them; as, for example, in the company of ants are found certain blind beetles, like *Claviger* (Myrmecophily), or some species of plant-lice, or even ants of other species and genera. But such cases of association correspond in part to the domestication of animals, or to slavery, as carried on by man. The ants keep the plant-lice in order to lick the sweet juice which is secreted in their honey-tubes; they steal the pupæ of other ants and rear them, to use them later as slaves. This state of things rests, consequently, not upon equal rights, since the one animal, in the present example the ant, brings about the association, while the other animal is passively led into it.

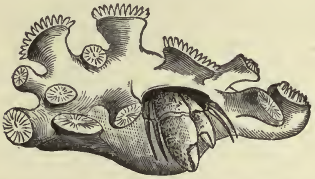


FIG. 113.—A colony of *Epizoanthus americanus* on the shell occupied by a hermit-crab. (From Verrill.)

An instance of most complete equal rights and true symbiosis is furnished us, however, by a hermit-crab and an actinian (fig. 113), *Eupagurus pubescens* and *Epizoanthus americanus*. Like every species of hermit-crab this also inhabits a snail-shell from the opening of which only his legs and pincers are protruded. Upon this shell an *Epizoanthus* becomes attached and by budding soon covers it with a colony of polyps. "After thus covering the shell it is not only capable of extending the aperture by its own growth, but has the power of entirely dissolving and absorbing the substance of the shell so that no trace of it can be found, though the form is perfectly preserved by the somewhat rigid membrane of the polyp." The advantage which the actinian derives from this symbiosis is clear: it gains a share of the food which the crab obtains. It is less clear what the crab gains by the association; however, the polyp is perhaps a protection to him, by means of its batteries of nettle cells, while by growth it increases the size of the 'house' occupied by the hermit and thus saves him periodic changes of abode.

Occurrence of Symbiosis.—That animals in general rarely live symbiotically with one another rests mainly upon the fact that the conditions of life of all animals to a certain point are similar or identical. They all take in compounds rich in carbon and nitrogen, decompose them, and, in the presence of oxygen, separate them into carbon dioxide, water, and oxidation products containing nitrogen. All animals consequently are competitors in the struggle for food. For the same reason, conversely, symbiosis between plants and animals is not at all uncommon. In particular there are certain lower algæ, the Zooxanthellæ, which often live in animals. The radiolarians contain with such constancy in their soft bodies green- or yellow-colored cells that for a long time these were regarded as constituent parts of the animal. Quite similar yellow and green cells inhabit the stomach epithelium of many actinians, corals, and even of many worms. The Zooxanthellæ are nourished by the carbon dioxide which is formed by the animal tissues, and breathe out oxygen, which in turn serves as food for the animal; further, they form starch and other carbohydrates, and there is nothing to prevent any surplus thus formed from becoming food material for the animal. Thus there is on a small scale that cycle of matter which exists on a grand scale in Nature between the animal and vegetable kingdoms. By aid of chlorophyl and of the chemical influence of sunlight the plants decompose water and carbon dioxide and form from them oxygen, which they breathe out, and compounds rich in carbon, which they store up in their tissues: they are *reducing organisms*. On the contrary, animals give off carbon dioxide and water, but take their oxygen from the air, and carbon compounds in their food; they use oxygen to break down the chemical combinations, to oxidize: they are *oxidizing organisms*. This explains why the favorable influence of plants upon animals ceases immediately when they change the character of their metabolism. With the disappearance of their chlorophyl moulds and bacteria lose the power of reducing carbon dioxide; they derive their food from other organisms and decompose this into carbon dioxide, water, etc.; like animals, they are oxidizing organisms, and consequently dangerous competitors. When they establish themselves upon the animal body, they almost always work injury to it; hence in animals they are the cause of many extremely dangerous ailments.

IV. ANIMAL AND PLANT.

Distinction between Animal and Plant.—The consideration of symbiosis has led us up to the fact that a distinction exists between plants and animals in the mode of metabolism, which may be expressed thus: plants usually take in carbon dioxide and give off oxygen, while animals breathe in oxygen and give out carbon dioxide. Hence it might be concluded that it is easy to discover differences which generally obtain between plants and animals, for, as a matter of fact, the laity are never in doubt in deciding to which realm of nature the more highly organized animals and plants, which are the only ones known to them, belong.

Doubtful Cases.—But the more one studies this question, the more difficult becomes its solution. The old zoologists indeed formed the conception that there are organisms which stand on the limits between the animal kingdom and the vegetable, and Wotton named these directly *zoophytes* or *plant-animals*. Now we know that Wotton's plant-animals are true animals with but a superficial similarity to plants; but, by means of the microscope, we have become acquainted with numerous lower organisms, and it is still doubtful in which of the two realms of nature these belong. As such may be mentioned the Myxomycetes and many Flagellata.

Physiological Distinctions.—If one wish to discover sharp distinctions between animals and plants, he may take into consideration on the one side *physiological*, on the other *morphological*, characters. Starting from the physiological point of view, Linnæus ascribed to plants only the capacity of reproduction and nutrition, but to animals the power of motion and sensation in addition. However, we know that vegetable, like animal, protoplasm is irritable and is capable of movement, as is shown by the active movements of the lower Algæ, the great sensitiveness of the *Mimosa*, and other plants; but further, we know that even many of the more highly organized animals, e.g., Crustacea (fig. 114), lose the power of locomotion and become fixed, and many fixed forms, e.g., the sponges (fig. 84), even under the closest examination appear immovable and unaffected by stimulation; thus we are led to abandon the idea that the so-called animal functions are to be regarded as accurate distinctions.

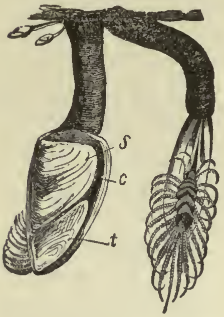


Fig. 114.—*Lepas anatifera.* (After Schmarda.) *c*, carina; *t*, tergum; *s*, scutum.

Metabolism not a Safe Criterion.—Even the difference in metabolism is by no means sufficient. Every plant has a double exchange of material. In its movements and other vital functions the vegetable protoplasm produces carbon dioxide and consumes oxygen; at the same time there goes on, under the influence of sunlight and of chlorophyl, the reduction of carbon dioxide and the giving off of oxygen. In chlorophyl-containing plants the reducing process preponderates so considerably during the day that there is evident, as the final result, the giving off of a greater quantity of oxygen, and only at night, when the reducing process becomes interrupted on account of the lack of sunlight, does the production of carbonic-acid compounds become perceptible. But the reducing processes become immediately preponderant if the chlorophyl be absent; chlorophylless moulds and bacteria have, therefore, the same metabolism, so far as carbon dioxide is concerned, as animals.

Cellulose not a Sure Test.—So also it is incorrect to say that only plants have the power to make cellulose, for cellulose is found in many lower animals, the rhizopods, and in the highly organized group of tunicates; according to recent investigations it appears to be found even among the arthropods.

Morphological Distinctions.—Turning to the morphological characteristics, multicellular animals and multicellular plants are readily distinguished, since the former in the germ-layers have a principle of cell arrangement peculiar to them. With the appearance of the gastrula each organism is undoubtedly an animal. But in unicellular animals the arrangement of the cells is lacking, and only the constitution of the single cell guides us. Now are there unmistakable morphological differences between the animal and the vegetable cell?

Plant-cells have a Cellulose Membrane.—In the structure of plant and animal cells an important distinction is found in the fact that the former has a cellulose membrane, but the latter is usually membraneless. To this distinction must be referred in the last analysis the widely different appearance of the two realms. Since the plant-cell is early surrounded with a firm coat, it loses a large part of its power of further changing its form; hence vegetable tissues and organs are uniform in comparison with the inconceivable multiformity which animal histology and organology disclose. The numerous higher stages of organization which the animal kingdom reaches, even in its lower classes, is in great part, indeed, the result of the fact that the cells of animals do not become encapsuled, but have preserved the capacity for more varied and higher development.

Transitions.—But even here transitions are found between the lower plants and animals. In the lower Algæ the cells have power to emerge from their cellulose membrane, and to swim about freely (fig. 115), before they encapsule themselves anew. On the other hand, most unicellular animals encyst; they pause in their ordinary functions of life, become spherical, and surround themselves with a firm membrane, in some cases even of cellulose. Since in both cases an alternation between the encapsuled and the free-living condition occurs, only the longer duration of the one or of the other can lead to a distinction. But here occurs the possibility that undifferentiated intermediate forms exist; their actual existence prevents, even yet, a sharp distinction between the animal and vegetable kingdoms.

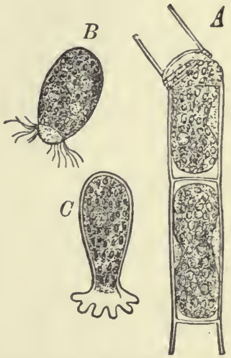


Fig. 115.—*Œdogonium* in spore-formation. (After Sachs.) *A*, a piece of the filament of the alga with escaping cell-contents; *B*, zoospore formed from the contents; *C*, zoospore fixed and germinating.

V. GEOGRAPHICAL DISTRIBUTION OF ANIMALS.

The Different Faunal Regions.—Even a superficial knowledge of the mode of distribution of animals shows that the animal fauna in different regions of the earth has an essentially different character. In part this difference of fauna is the immediate result of climatic differences. The polar bear, arctic fox, eider-ducks, and many aquatic birds are restricted to the polar zones, because they cannot endure more than a certain degree of warmth; on the other hand, the larger species of cats, the apes, the humming-birds, etc., occur only in tropical or sub-tropical regions, because they are not sufficiently protected against cooler weather.

Climate not the Only Factor.—If climate were the sole factor determining distribution, the faunal character of two lands which have similar climatic conditions would be essentially the same; conversely, the separate regions within a continuous territory extending through several climatic zones must have quite different faunas, according as they are nearer the equator or the poles. But such is not the fact; two tropical countries may differ more widely in the characteristics of their fauna than the hot and cold regions of one and the same country.

Factors in Distribution.—Modern zoology endeavors to explain these peculiar conditions by regarding the present distribution of animals as the product of two factors: the gradual changes of the animal world, and further the gradual changes of the earth's surface on which the animals are distributed. The history of the earth as disclosed by geology shows two facts: (1) that the connexions between parts of the earth have varied greatly; that, for example, at a time when the Mediterranean had not yet reached its present extent, Morocco, Algiers, Tunis, and Egypt were more closely united with the European coast of the Mediterranean than with the southern part of the African continent separated from them by the Sahara; (2) that considerable variations of climate have taken place: there prevailed in Europe in the tertiary period a subtropical climate which rendered possible the existence of animals which now occur in Algeria (lions). But later a glacial period began, which introduced over a wide area of the European continent the conditions of arctic life, and consequently a fauna of northern animals (reindeer). Hand in hand with the geological changes went changes in the animal world, the then existing species dying out under the change of conditions, or forming new species through gradual variations. Thus the distribution of animals constitutes an extremely complicated problem, the solution of which necessitates comprehensive preliminary work. It must be known with certainty how the connexions between the continents and the climates have changed, particularly in the later geological periods; further, we must study, not only how animals are distributed over the earth's surface at the present time, but also how they were distributed in earlier times. Finally, by means of comparative anatomy and embryology we must have clear and detailed ideas of the relationships and interrelationships of animals.

It will be an extremely long task to solve all the problems of the subject here sketched in outline. What has been investigated thus far can only be regarded as a preliminary proof that zoology with its prevailing views of the changes of animals and of the earth is on the right track. It would be a test of the correctness of this view if it were proved that the faunal resemblances of two countries depends, in the first place, upon how long they have been in close connexion with each other, consequently allowing an interchange of the animals inhabiting them. Two regions, separated early in the earth's history and never again connected, must have greater differences in faunal characters than two lands still connected or only recently separated. It is instructive when we travel in the northern hemisphere and find in widely separated regions strikingly similar faunæ, while under the equator or in the southern hemisphere under the same conditions striking differences are seen. This is explained on the hypothesis that in all past periods as now the land masses of the northern hemisphere have been closely connected, while the parts of the continents extending to the south—aside from hypothetical temporary connexions between South America, Africa, and Australia—have been separated through most of the earth's history.

In carrying out more closely the points of view mentioned, students of distribution have attempted to mark off the great faunal areas of the earth, the faunal provinces or regions, and within these again less important divisions, subregions. These provinces have been based chiefly upon the distribution of mammals, less upon that of birds and other animals; for the distribution of mammals is chiefly determined by those changes of the earth's surface which are best known geologically and possess most interest. Elevation or depression of the earth's surface often opposes impassable barriers to most mammals: rising, if it lead to the formation of glaciered mountain-chains; sinking, when arms of the sea are formed, which, even if only narrow, interpose between two hitherto connected land areas straits which are impassable for most mammals. Birds and insects which fly well are less affected by all such changes of the earth's surface; the majority of them can fly over arms of the sea and mountain-chains, for there are birds which can even cross the Atlantic Ocean.

The Six Primary Regions.—Of the systems of animal geography proposed up to the present time, the divisions advocated by Sclater and Wallace finds most favor. These English scholars distinguish the six following primary regions: (1) the *palæarctic,* comprising all Europe, northern Africa as far as the Sahara, and northern Asia as far as the Himalayas; (2) the *Ethiopian*, all of Africa south of the Sahara; (3) the *oriental,* including upper and farther India, southern China, and the western Malay Islands; (4) and (5) the *nearctic* and the *neotropical* regions, which make up the American continent and are divided by a line drawn at about the northern border of Mexico; (6) the *Australian,* in which, besides Australia itself, are included the larger and smaller islands of the Pacific Ocean and the eastern Malay Islands, east of Celebes and Lombok.

(1) The Australian region is most sharply distinguished from all the others and by many is set apart as a distinct division called 'Notogæa.' Its isolated geographical position together with the fact that it has long been separated from other countries (apparently since the beginning of the tertiary) explains the fact that only the oldest mammals, the monotremes and marsupials, have entered the region, while the placental mammals have not been able to follow. While the marsupials, which in the secondary period also inhabited the northern hemisphere, were replaced there in tertiary times by the placentals, they were able to develop farther in the Australian region. Australia and the adjacent islands are thus the land of marsupials, which have persisted elsewhere only in South America (*Cœnolestes,* Didelphidæ), the opossum ranging north into the United States. On the other hand, at the time of discovery Australia lacked all placental mammals except those (whales, dugong, seals, bats) which were not restricted by water and the Muridæ, easily transported on floating wood. Two larger mammals, the wild dog or dingo (*Canis dingo*) and the pig of New Guinea (*Sus papuanus*), may have accompanied man, this being the most probable for the dingo in spite of the fact that his remains occur in the pleistocene along

with those of the giant marsupials. Further peculiarities of the Australian region are the birds-of-paradise in New Guinea, the egg-laying mammals *Ornithorhynchus, Echidna,* and *Proechidna,* and the cassowaries and the Australian ostrich (*Dromæus novæ-hollandiæ*).

It is easily understood that the isolated island groups of the South Sea (Polynesia) have developed many faunistic peculiarities, as well as that an exchange of forms may have taken place between the islands of the oriental province and the islands faunally related to Australia, and that 'Wallace's Line' is not so sharp a boundary as it was once thought to be (extension of marsupials into Celebes, of placentals into the Moluccas). On the other hand the distinctness of New Zealand needs mention. It is distinguished from Australia by a large number of peculiar birds (*Apteryx* and the extinct Dinornithidæ), reptiles (the ancient *Sphenodon*), and molluscs. If the bats and mice—unimportant in matters of distribution—be excepted, New Zealand lacks all native mammals, even marsupials.

(2) The neotropical province (South and Central America) is, next to Australia, the most sharply characterized, and, like that region, has been set aside as a special division 'Neogæa,' especially when considered with reference to its geological history, which shows that during the cretaceous and early tertiary time it was separated from North America by the sea and had developed a peculiar fauna (e.g., gigantic edentates, no carnivores). These peculiarities disappeared towards the end of the tertiary by the entrance of carnivores and ungulates from the north and an extension of the edentates to the northern hemisphere. To the Neogæa belong the platyrhine apes, the catarrhine to the Old World. Characteristic edentates are the armadillos, sloths, and ant-eaters; the marsupials are represented by the opossums and *Cænolestes;* among birds the humming-birds, toucans, the peculiar Cotingidæ, Tanagridæ, Tinamous, Palamedidæ, Rhea, etc. The almost entire absence of insectivores and the considerable development of rodents (cavies, agoutis, chinchillas) are noteworthy.

The four remaining provinces are still closely connected geographically and form a third great division, 'Arctogæa,' characterized by the entire absence of platyrhine apes, monotremes, and, except the North American opossum, of marsupials. In the secondary and tertiary times the northern parts of these lands were connected and an interchange of faunas occurred, this being the easier on account of the extension of the warm climate to the far north. Hence many unite the palæarctic and nearctic provinces into a 'holarctic' province.

(3) The nearctic region has peculiar to it three mammalian families, the prong-horned antelope, the opossums, and the Haplodontæ; of the group of Amphibia, the Sirenidæ and Amphiumidæ. The Nearctic is to be distinguished from the nearest related palæarctic region through the crowding in of neotropical forms like the raccoon, opossum, humming-birds, etc.

(4) The palæarctic region covers the greatest area and consequently abuts upon many other provinces. Hence there exist on the one side important differences between the various local faunas, which are conditioned by climate and great distances, but on the other it explains the fact that the palæarctic region has no peculiar families. The families which here have reached a great development are the deer, cattle, sheep, and camels; especially conspicuous genera are the chamois, squirrel, badger, and marmot.

(5) The Ethiopian region has many animals found only there; among these the hippopotamus and giraffe, the aardvark, and, if we include Madagascar, the lemurs are most characteristic. To these are added a rich development of antelopes and zebras and the gorilla and chimpanzee. Equally noteworthy is the entire absence of striking families and genera, such as the bears, moles, deer, goats, tapirs, sheep, the true cattle and swine, provided they have not been domesticated and introduced.

Within the region the island of Madagascar occupies a remarkable position. This island is the land of lemurs and Insectivora; no land is so rich in lemurs, as the majority of the genera live exclusively in Madagascar. On the other hand the large beasts of prey, the cats, hyenas, dogs, and the bears (which, however, do occur in Africa), all the true apes, antelopes, elephants, and the various species of rhinoceros are absent. Consequently, since Madagascar is distinguished quite conspicuously from Africa, many zoologists separate the island from the Ethiopian region; many even give it the rank of an independent province.

(6) The oriental region contains, next to Madagascar, the most lemurs; among which the Tarsidæ and Galeopithecidæ (the latter often considered an insectivore) are exclusively oriental. Remarkable inhabitants of the province are the gibbons and orang-utans, the musk-deer, numerous families and genera of birds.

Arctic and Antarctic Provinces.—Of late the view has gained ground that, besides these six, two other, circumpolar, provinces must be distinguished, the arctic and the antarctic. Both have a fauna consisting of few species but numerous individuals, of which the auks, polar bear, reindeer, and arctic foxes are characteristic of the northern or arctic region, the penguins and the entire absence of land mammals of the antarctic.

The Distribution of Aquatic Animals.—Since most seas are connected, the faunal regions cannot be distinguished so sharply as in the case of the land faunas; conspicuous differences are present only when two oceans are separated by continents extending far to the north and south; such, for example, exist between the Red Sea and the geographically neighboring Mediterranean, between the east and west coasts of North America, even where they are separated only by the narrow isthmus of Panama. Then, too, considerable differences may exist where currents of greatly different temperatures meet.

Changes in the Fauna Conditioned by Depth.—Much more remarkable in the marine fauna are certain differences brought about by the changes of the conditions of life in the different depths of the sea. A *deep-sea fauna*, a *coast fauna*, and a *pelagic fauna* can be distinguished. The coast fauna embraces the animals, some free, some fixed, which inhabit the plant-covered rocky or sandy shore to a depth of a few hundred feet. The deep-sea fauna swims, creeps, or is fixed at the bottom of the ocean at depths of 1000 to almost 9000 meters; it is distinguished from the coast fauna in part by its archaic character, for here very often genera and entire groups of animals exist, like the Hexactinellidæ, crinoids, certain starfishes and sea-urchins, etc., which for a long time were chiefly known through fossils from earlier geological ages.

The Plankton.—The pelagic animal world comprises all forms which swim freely in the water, the 'plankton'; here belong many cœlenterates, medusæ, and ctenophores, entire groups of Protozoa, like the radiolarians, many Crustacea and crustacean larvæ; of the molluscs the heteropods and pteropods. These animals live either at the surface of the sea itself or floating at greater or lesser depths, to 8000 meters or even more. Usually they are gelatinous and of glasslike transparency; this must be regarded as sympathetic coloring and adaptation to the transparency of the water.

Distribution of Fresh-water Animals.—In fresh water two groups of animals must be distinguished, of which the one comprises mainly the more highly organized forms, the molluscs, fishes, and Crustacea, the other the lower animal world. The distribution of the former is mainly determined by the same factors which influence terrestrial forms; the distribution of the latter, however, is cosmopolitan. The same infusorians and rhizopods, copepods, fresh-water sponges and polyps which occur in America seem to be distributed over the entire earth. This is connected with the fact that all these animals have resting stages in which they endure desiccation. The resting stage, be it as a hard-shelled egg or as an encysted animal, may be borne about by the wind, or may be carried with the mud by aquatic birds, and upon again reaching the water resume its active state.

VI. DISTRIBUTION OF ANIMALS IN TIME.

It is the province of a special science, paleontology or paleozoology, to treat of the character and distribution of animals in the earlier periods of the earth's history, but since it is necessary to draw upon paleontological facts to understand the living forms an outline of the geological periods with the characteristic animals may be given here.

I. Azoic or Archean Era.

No organisms are certainly known from this age. The animal nature of *Eozoon canadense* of the Laurentian beds, once referred to the Foraminifera, is more than doubtful.

II. Palæozoic Era.

1. Cambrian.
2. Silurian.
3. Devonian.
4. Carboniferous.
5. Permian.

The oldest paleozoic period, the Cambrian, contains only invertebrate fossils: trilobites, gigantostraca, cystoids, nautiloids, gasteropods, and a few lamellibranchs. Trilobites, cystoids, gigantostraca, and the blastoids and tetracoralla, which appear in the Silurian, reach their culmination and become extinct in the paleozoic. Fishes appear in the Silurian, and acquire a great development in the Devonian. The earliest Amphibia come from the carboniferous, the reptiles appear in the Permian.

III. Mesozoic Era.

1. Triassic.
2. Jurassic.
3. Cretaceous.

The mesozoic era was the age of reptiles, which were represented by numerous forms, some of gigantic size; most of them becoming extinct in the cretaceous. The first mammals appear in the triassic, the birds in the Jurassic. Among the invertebrates the ammonites, which appeared in the Devonian, reached their greatest development and became extinct in this era.

IV. Cenozoic Era.

(*a*) Tertiary.
  1. Eocene.
  2. Oligocene.
  3. Miocene.
  4. Pliocene.

(*b*) Quaternary.
  5. Pleistocene.
  6. Recent.

In the tertiary all of the now living orders of mammals and birds appeared, among them man, whose remains have been traced with certainty to the pleistocene.

SPECIAL ZOOLOGY.

SINCE comparative anatomy and the theory of evolution have made their impression upon systematic zoology one recognizes in classification not only a means of arranging the species, but also the possibility of expressing the relations which the larger and smaller groups bear to each other. The solution of these problems demands an accurate knowledge of comparative anatomy and embryology and a complete knowledge of animal forms based upon them. We are yet far from such a knowledge, farther with regard to some groups than others, and as a consequence systematic problems are not all equally advanced towards solution.

In general it may be said that certain natural groups are recognized: (1) Chordata; (2) Mollusca (after the elimination of the Brachiopoda); (3) Arthropoda; (4) Echinoderma; (5) Cœlenterata (after the separation of sponges); (6) Protozoa. On the other hand, it is yet uncertain exactly how to regard the worms, brachiopods, polyzoa, and a few other forms. The general tendency is to distribute the worms into at least three branches (flat worms, round worms, and annelids) and to unite the Polyzoa and Brachiopoda in a branch of Molluscoida. In this way groups poor in species and of little importance in a general account of the animal kingdom are placed on the same basis as the large and exceedingly important groups of vertebrates, arthropods, and molluscs, and thus obtain, especially in the eyes of the beginner, an importance which does not belong to them. It therefore seems better in an elementary work to pursue a more conservative course.

PHYLUM I—PROTOZOA.

All of the Protozoa are small; some may be seen by a sharp eye as minute points, but the majority are so minute that they are invisible except with a microscope. On the other hand, there are a few which have a diameter to be measured by millimeters, this being especially the case where hundreds of individuals are united in colonies.

This small size is a necessary result of the fact that the Protozoa are single-celled animals. Like all cells they consist of that peculiar substance, protoplasm, and they have the further cell attribute, the possession of one or more nuclei. Being unicellular, it follows that they lack true tissues and true organs. They lack alimentary canal, nervous system, sexual organs, etc. The fundamental functions of nourishment, sensation, movement, and reproduction are performed more or less directly by the protoplasm.

In nutrition, in so far as it is not produced by substances in solution, foreign particles pass into the protoplasm and are digested by it. They usually lie during digestion in special collections of fluid, the food vacuoles (figs. 120, 144, etc, *na*), more rarely in the protoplasm itself. All indigestible portions are cast out after a time. This taking in and casting out of foreign matter can take place in the lower Protozoa at any point of the surface, while in the more highly organized species there are definite openings which according to analogy with many-celled animals are spoken of as mouth and anus, or more precisely, *cytostome* and *cytopyge*. The mouth may connect with a tube, the œsophagus or *cytopharynx*, which ends free in the protoplasm.

Structures may occur within the protozoan cell which recall the organs of higher animals, and which are called cell organs. While motion is usually produced by the protoplasm and its processes—pseudopodia, flagella, and cilia—there are Protozoa, like *Stentor* and the Vorticellidæ, which have true muscular fibrillæ. The sensitiveness to light is often increased by the formation of an eye spot, a small pigment body in which even a lens may occur. More constant of cell organs are the contractile vacuoles (fig. 116, etc., *cv*), structures rarely absent from fresh-water species, but commonly lacking from marine forms. These are distinguished from the food vacuoles by three characters: they have a definite place in the cell; their number is approximately constant in most species; they exhibit extremely constant phenomena. The walls contract and empty the fluid contents to the exterior, often through a special duct. When one empties it completely disappears and is formed again anew in a short time, and is filled with fluid from the surrounding protoplasm. It thus resembles the contractile vacuoles in the water vascular system (excretory organs) of the worms to be described later. Apparently the contractile vacuoles are for the elimination of injurious substances in solution produced by the vital processes, among them possibly carbon dioxide, like a respiratory organ.

Apparently all the vital functions are under the control of the nucleus. Experiments show that Protozoa, artificially deprived of their nuclei, perform their functions incompletely and soon perish, while fragments containing a nucleus remain alive. Young Protozoa usually have a single nucleus, and many have but one throughout life; but others early become multinucleate. Such multinucleate forms are frequently regarded as cell complexes or syncitia, but unnecessarily, for aside from the fact that in animal and plant histology polynucleate masses of protoplasm are regarded as cells, this term makes a distinction between the uni- and the multi-nucleate forms, which does not correspond to the actual relations, since the phenomena of both are completely alike.

Reproduction is accomplished exclusively by fission or budding, and under suitable conditions, such as abundance of nourishment, occurs so rapidly that many Protozoa inside a few weeks can number their descendants by millions. Many divide in the free state while they are creeping or swimming about; others become encysted before division. They become spherical and secrete a protecting membrane around themselves (figs. 121, 122). Encysted individuals usually divide into more than two pieces, in four, eight, or even many hundreds of reproductive bodies. It frequently happens that multinucleate species divide into as many parts as there are nuclei.

In the Protozoa may occur a fusion of individuals—conjugation—which in many respects has much similarity to the process of fertilization in Metazoa and in plants. In some (conjugation of many Rhizopods) this does not correspond to true fertilization, since only the protoplasm unites (*plastogamy*), while the fusion of nuclei (*caryogamy*) necessary to fertilization does not occur. In others a fusion of nuclei takes place. In the cases which have been accurately studied there has been seen, before the fusion of the nuclei, a process comparable to the formation of the polar globules in the egg, to this extent, that in each of the conjugating individuals the nucleus divides twice and of the products of division only one, the nucleus intended for caryogamy, persists while the others (polar globules) degenerate.

These cases of true fertilization permit of great diversity. The conjugating individuals can be equal in size (most Infusoria, many Rhizopoda), or there is a disparity in size (sexual dimorphism), in which smaller and consequently more mobile 'males' (microgametes, zoospores) fertilize the larger fixed or slowly moving 'females' (macrogametes, oospores) as in *Volvox globator*, Vorticellidæ, and many Sporozoa. In conjugation of individuals of equal size there is frequently a mutual fertilization—A fertilizes B, and is in turn fertilized by B—after which the animals separate (most Infusoria, Gregarines, *Noctiluca*).

Twenty years ago it could be laid down as a universal fact that the Protozoa in contrast to the Metazoa lacked sexuality. In the mean time observations on Protozoa belonging to different classes, even the Rhizopoda, have so increased that the conclusion is that fertilization occurs in all Protozoa, although the rarity of the process in many species renders the complete demonstration difficult. Still there remain certain interesting differences from the Metazoa. The Protozoa lack special sexual cells —eggs and spermatozoa. On the contrary, the whole body functions as a sexual cell. Further, the relations of fertilization to reproduction are not the same as in the Metazoa. It does indeed occur (swarm-spore formation in *Noctiluca*, formation of pseudonavicellæ in gregarines) that fertilization precedes rapid division, but much more commonly fertilization is the result of rapid division and a cause of slower reproduction (*Infusoria*) or even of complete rest (*Actinosphærium*, *Actinophrys*, *Volvox*). One can therefore only speak of fertilization, not of sexual reproduction, in the Protozoa. These facts are of great importance in the consideration of the nature of impregnation, for they show that it has not only the purpose of stimulating the developmental processes, but that it accomplishes other functions, and that these functions, obscure as they at present are, are the more important since they are the more primitive and the more widely distributed.

With *Noctiluca*, many Sporozoa, and perhaps in Rhizopods a period follows impregnation in which the division ('sexual reproduction') has a special character (swarm-spore formation in *Noctiluca*, formation of sporoblasts and sporozoites in the Sporozoa) and differs from the customary 'vegetative' reproduction. This alternation of methods of reproduction recalls the alternation of generations of the Metazoa and is called by the same name.

The Protozoa with thin small and soft protoplasmic bodies are but little if at all protected against drying up, and therefore they are aquatic. A few forms, like *Amœba terricola*, are terrestrial, and these only occur in moist places. Salt and fresh water, of the latter stagnant pools rich in vegetation, are the favorite places for Protozoa. The fresh-water forms are cosmopolitan, so that the forms in the most diverse lands are very similar. This depends upon certain peculiarities. The fresh-water Protozoa can become encysted independent of reproduction, and in the encysted stage can endure times of unfavorable conditions such as lack of food, freezing, or complete evaporation of the water. When thus protected they may be blown about by the wind or carried far on the feet of birds. Hence it is that one group bears the name Infusoria, for if dry earth or dry plants (*e.g.*, hay) be soaked in water and this infusion allowed to stand for some time, a more or less rich Protozoan fauna will develop in it. The encysted animals in the earth or on the plants are awakened by the moisture to new life and leave the cyst. Spontaneous germination, as was once believed, does not occur here, for if one sterilize the materials and prevent the entrance of germs the water will remain uninhabited.

Historical.—On account of their practical invisibility the Protozoa were unknown until 1675; they were discovered in infusions by the Dutch Leeuwenhoek, the discoveror of the microscope. Wrisberg in the eighteenth century called them Animalcula infusoria—infusion animals, and Siebold in the century just closed gave them the name Protozoa. The proposition of Haeckel to place a portion of the Protozoa in a kingdom Protista between animals and plants has found but little acceptance. In the accounts of the structure the views of Dujardin and Ehrenberg were long at variance. Ehrenberg maintained with all confidence that the Protozoa like all animals possessed the most important organs, alimentary canal, nervous system, muscles, excretory and sexual organs. Dujardin denied all this and ascribed to the Protozoa only a single homogeneous substance, 'sarcode' (p. 60) which was sufficient to produce all vital phenomena. Dujardin's view later found important support in Siebold's discovery that the Protozoa were unicellular. Still for a long time Ehrenberg's ideas persisted in various modified forms and were not totally overthrown until after the middle of the nineteenth century. The fact that there are unicellular animals without organs and yet capable of existence was an extremely valuable addition to knowledge, for it not only broadens our conception of animal life, but it furnishes for the theory of evolution from simple organisms the strongest link in the chain, the first of the series.

The different appearances of Protozoa depend upon the grade of organological and histological differentiation. Since these are most prominent in the nourishing and locomotor structures, these become important in subdividing the group. The organs for these purposes—pseudopodia, flagella, cilia—furnish the basis for the differentation of these classes, to which are added forms—the class of Sporozoa—modified by parasitism.

Class I. Rhizopoda.

In the lowest position in the Protozoa must be placed those organisms which lack permanent structures for locomotion and nourishment, but in which the protoplasm of the body performs these functions. The term Rhizopoda refers to the fact that the protoplasm sends out root-like processes—false feet or pseudopodia—for locomotion and for taking nourishment. These differ from true appendages in that they are not constant cell organs, but are formed according to demand and again disappear. A pseudopodium arises when the protoplasm streams to one point of the body and extends as a process beyond the surface. Since the process becomes attached and draws the body after it, or since the protoplasm of the body may flow into it, a slow change of place occurs. Thus the process disappears and is absorbed in the organism, and new pseudopodia are formed at other places which after a time are retracted in turn. This type of locomotion is called amœboid after the *Amœba,* in which it was first accurately studied. When the Rhizopoda in their wanderings meet particles of nourishment, they enclose them with their protoplasm and take them into the interior of the body (fig. 116, *N*).

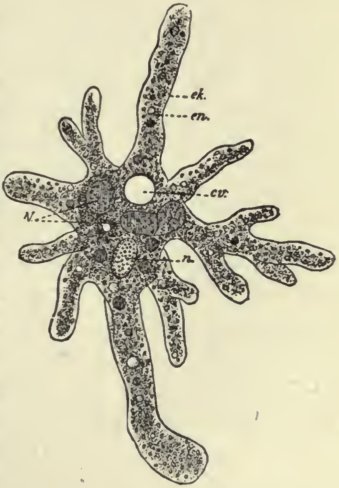


Fig. 116. — *Amœba proteus.* (After Leidy.) *cv*, contractile vacuole; *en*, entosarc; *ek*, ectosarc; *n*, nucleus; *N*, food-body.

The form of the pseudopodia is approximately constant for each species, but as a whole very variable, so that it may be used not only for separating species but families and larger groups. On the one hand, there are finger-like pseudopodia (fig. 116), on the other, those of such delicacy that even under strong magnification they appear like fine threads (fig. 117). Between these two extremes are many intermediate forms. Thread-like pseudopodia usually branch, and when the branches meet they may fuse and form anastomoses, from which it follows that it is not true, as was once supposed, that the pseudopodia are covered by a membrane.

The fine granules of the protoplasm can enter the pseudopodia and produce here, as they move back and forth, the phenomenon of 'streaming.' Since foreign particles, like grains of carmine taken up by the protoplasm, can participate in this streaming, it follows that the movements depend not upon the granules but on the protoplasm itself. We have already used the fact (p. 62) that granules in the finest thread can move in opposite directions at the same time, to demonstrate the extraordinary complexity of protoplasmic structure.

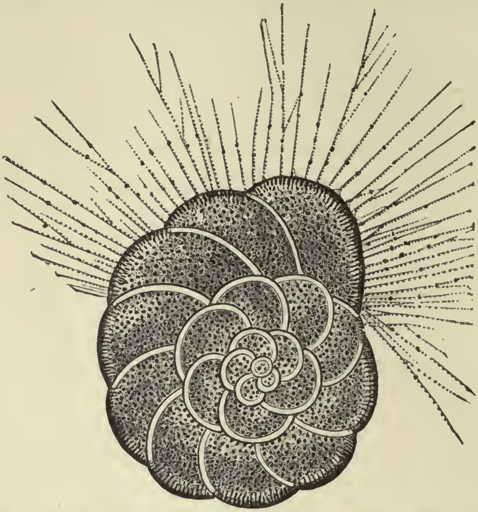


FIG. 117.—*Rotalia freyeri.* (From Lang, after M. Schultze.)

When Rhizopoda, in the free or encysted condition, increase by division, the division products frequently exchange the amœboid motion for that of the Flagellata, and become flagellate spores or zoospores. The body becomes oval and develops, on the anterior end which contains the nucleus, one or more flagella, which move more energetically than pseudopodia, and are permanent as long as the zoospore stage persists (fig. 121). Since many Protozoa possess flagella along with pseudopodia, the boundary between Rhizopods and Flagellates is not distinct (fig. 118).

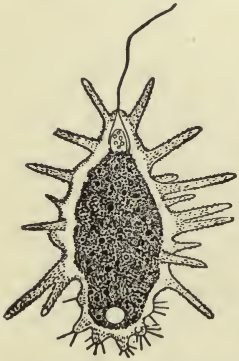


FIG. 118.—*Mastigamœba aspera.* (After F. E. Schulze.)

The Rhizopoda form an ascending series in which the systematic characters become more and more pronounced; such are the assumption of a definite form, as in the Radiolaria and Heliozoa, the formation of a skeleton of regular character, as in the Thalamophora, or the development of a peculiar reproduction, as in the Mycetozoa. At the bottom stand the Monera and the Lobosa whose characters are mostly negative, for neither form, skeleton, nor reproduction affords systematic distinctions.

Order I. Monera.

The most important character of the Monera is the lack of a nucleus. As with other negative characters this is somewhat uncertain. In many cases, especially when the protoplasm is filled with chromatin granules, the nucleus is recognized with difficulty, and hence animals have been described as anucleate in which the nucleus was overlooked. The number of 'Monera' was formerly very great, but has diminished with the development of microscopic technique. So it is possible, even probable, that, in the few forms now remaining in the group, the nucleus has merely escaped observation. On the other hand there are several theoretical reasons which support the idea of anucleate organisms. It is easier to suppose that with the appearance of life there were organisms consisting of but a single substance than that these organisms had nucleus and protoplasm already differentiated. Several species of *Protamœba* are placed in the Monera.

Order II. Lobosa (Amœbina).

Lobosa are primitive Rhizopoda with one or several nuclei. The species of *Amœba*, forms which owe their name to their constant change of shape, are typical (figs. 116, 119). This change of form is due to the formation and disappearance of a few finger-like (lobose) pseudopodia. Body and pseudopodia consist of two layers, a soft granular inner entosarc (*en*) and a firmer, clear, outer ectosarc (*ek*). In the entosarc is usually a single (sometimes several) nucleus (*n*), which is vesicular, and contains either one large or several smaller nucleoli. A contractile vacuole is usually present. Reproduction occurs by division (fig. 119), and in some instances encystment has been observed, the protoplasm dividing into many hundred small amœbæ.

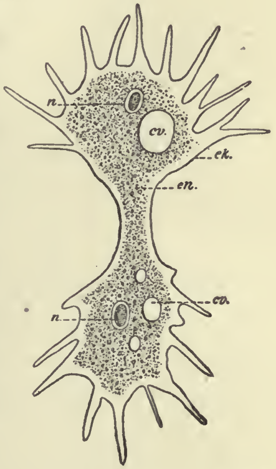


FIG. 119.—*Amœba polypodia* in division. (After F. E. Schulze.) *cv*, contractile vacuole; *ek*, ectosarc; *en*, entosarc; *n*, nucleus.

Most Lobosa occur in fresh water; the larger forms, like *Pelomyxa palustris* (2 mm. in diameter) live in the ooze of pools, the smaller, like *Amœba proteus* and *A. princeps*, on plants or free in the water. The very small *A. terricola* lives in moist earth. There are also parasites among the Amœbæ, like *A. coli* (0.02 to 0.035 mm. large), rare in colder climates, frequently observed in the tropics in liver abscesses and in ulcers of the colon of men ill with dysentery, and perhaps the cause of the disease. Some of the Monothalamia (p. 198) are sometimes referred to the Lobosa.

Order III. Heliozoa, Sun Animalcules.

The Heliozoa owe their name to the shape of the body, with the pseudopodia arranged like rays. In the pseudopodia are a firm axial thread forming a skeleton and a thin coating of protoplasm. Branching and anastomoses of the pseudopodia are rare, and usually occur only when the radial arrangement is modified by pressure. The axial threads frequently converge at the centre of the body. Here lies a granule, the centrosome separated from the nucleus, which plays an important part in division. The body consists of cortical and medullary portions (fig. 120), distinguished by differences in the protoplasm, but not separated by membrane. In the cortex are the contractile vacuoles (*cv*); the medulla contains the usually single nucleus. Among the polynucleate forms is the largest and one of the most beautiful of fresh-water species, *Actinosphærium eichhorni*. Many

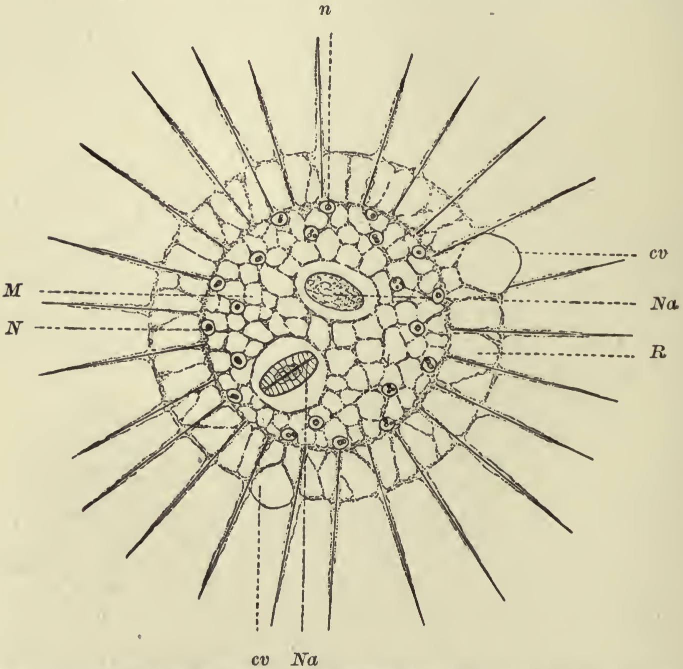


FIG. 120.—*Actinosphærium eichhorni*. *M*, medullary substance with nucleus (*n*); *R*, cortical substance with contractile vacuoles (*cv*); *N*, food-body.

Heliozoa possess a silicious skeleton, which may be a lattice-work sphere (fig. 121), needles radially arranged or placed tangentially. The forms without skeletons are few, but these have the power (fig. 122) of forming silicious envelopes during encystment.

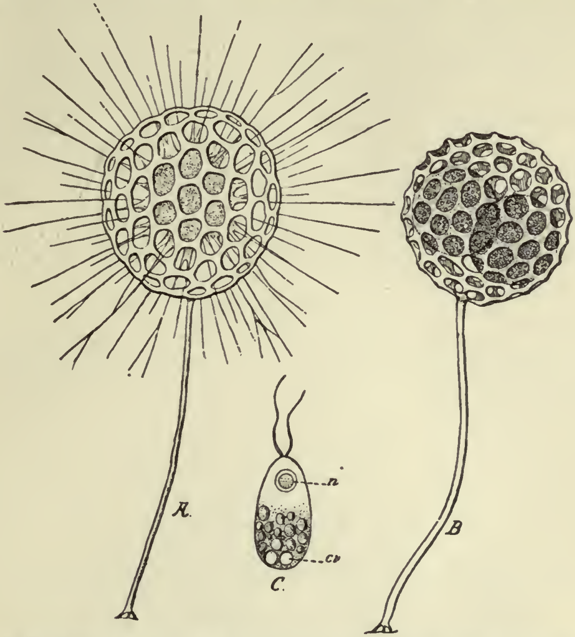


Fig. 121.—*Clathrulina elegans.* *A*, with extended pseudopodia; *B*, divided into two cysts; *C*, zoospore; *n*, nucleus; *cv*, contractile vacuole.

Reproduction takes place by division, and one or both moieties may become swarm spores, *i.e.*, assume an oval form bearing at one pole one or two flagella (fig. 121, *C*). These swarm spores become widely distributed by the flagella before they resume the spherical shape, lose their flagella and form pseudopodia. It frequently occurs that several Heliozoa of the same species become connected by protoplasmic bridges, and so form unions of from two to ten individuals. True fertilization preceded by a kind of polar-globule formation has only been observed in *Actinophrys sol* and *Actinosphærium eichhorni.*

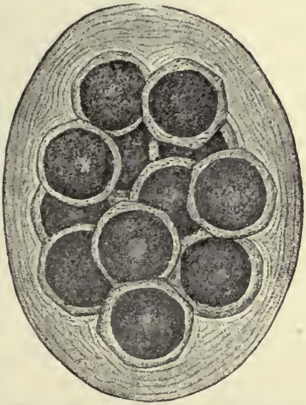


Fig. 122.—Cyst with germinal spheres of *Actinosphærium eichhorni.* (After F. E. Schulze.)

Forms with skeleton and those without are distinguished. To the first belong *Clathrulina elegans*, with a spherical lattice-work skeleton supported on a stalk (fig. 121). *Acanthocystis turfacea*, skeleton of radial, branching needles. To the forms without skeleton belong first *Actinosphærium eichhorni*, as large as a pin-head, milk-white, protoplasm foamy from the numerous fluid vacuoles, the different sizes of which markedly distinguish cortical from medullary proportions. The contractile vacuoles are in the cortex, the nuclei in the medulla. In encystment the foamy appearance and most of the nuclei are lost, and a cyst is formed with numerous uninucleate daughter cysts. Each daughter cyst divides into secondary cysts which, after the formation of polar globules, fuse (fertilization) and produce germ spheres. From these then escape, after a long rest, the young *Actinosphæria*. The reproduction of *Actinophrys sol*, a smaller form, is essentially similar.

Order IV. Radiolaria.

The Radiolaria, the most beautiful and most highly organized of the Rhizopoda, strongly recall, in their appearance, the Heliozoa. They are spherical, only rarely by flattening converted into disks, or by unequal growth into conical or lobular shapes.

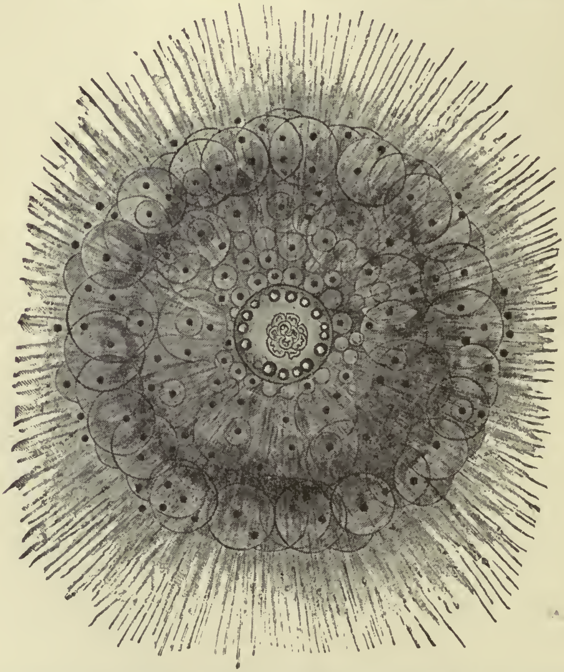


FIG. 123.—*Thalassicolla pelagica.* In the centre the nucleus with coiled nucleolus, around it the central capsule with oil globules; still outside the extracapsular soft body with vacuoles (extracapsular alveoli), yellow cells (black) and pseudopodia.

A second resemblance lies in the delicate pseudopodia, often with an axial filament. The distinguishing characteristic is the central capsule. This is the central portion of the body surrounded by a membrane, outside of which is the extracapsulum. The central capsule is the most important part of the animal. If it be dissected out from the extracapsulum it not only lives but regenerates the lost parts, while the extracapsular portions die. Since the protoplasm of both parts is identical, the difference in regenerative powers can only depend on the nuclei, which are confined to the central capsule.

The central capsule may be uni- or polynucleate. In the first case the nucleus (fig. 123), a vesicle of appreciable size, lies in the centre of the capsule, in the others the capsule is thronged by hundreds of small homogeneous nuclei. All Radiolaria are uninucleate in the young stage, and only at the time of swarm-spore formation polynucleate. The fact that certain species have almost always one nucleus, while others usually have many, is explained in the first case by the long continuance of the uninucleate condition, only giving place to the polynucleate condition just before the formation of swarm-spores, while in the second the polynucleate condition is reached early. In the central capsule are also included various deposits which serve as food during reproduction, such as concretions, oil globules, etc.

The membrane surrounding the central capsule is either perforated on all sides by numerous pore-canals or by small openings in certain places. Through these pores and openings the intracapsular protoplasm passes out and spreads itself in the extracapsulum. This consists of a gelatinous mantle through which the protoplasm extends as a fine network before it forms pseudopodia on the surface. In the larger Radiolaria it contains vacuoles (extracapsular alveoli) developed in the protoplasmic net (fig. 123).

With few exceptions the Radiolaria possess skeletons of wonderful beauty; latticed spheres, single or one within another, and bound together with radial rods (fig. 85), frequently ornamented on the outer surface with spines, or latticed discs, helmet-like or cage-like structures (fig. 124) or spongy structures. In other cases occur rings, tubes, spines, which meet

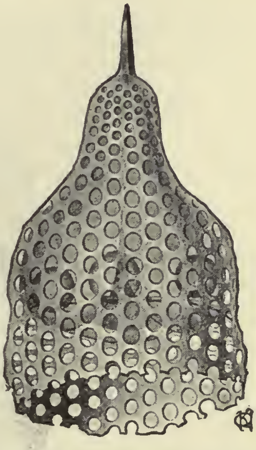


Fig. 124.—*Eucyrtidium cranioides.* (After Haeckel).

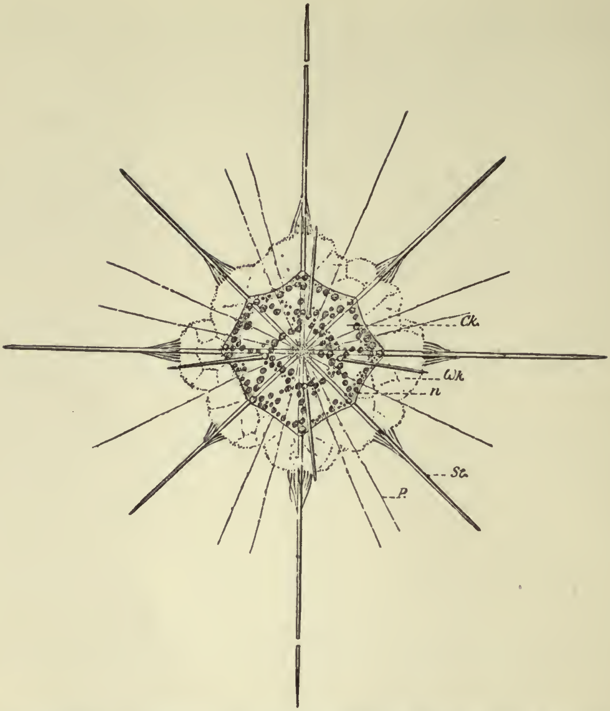


Fig. 125.—*Acanthometra elastica.* *ck*, central capsule; *n*, nucleus; *p*, pseudopodia; *St*, spines; *Wk*, extracapsulum.

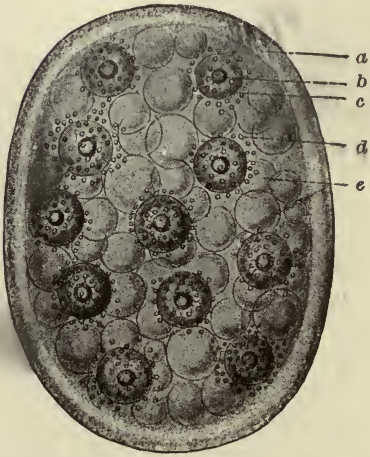


Fig. 126.—*Collozoum inerme.* *a*, jelly; *b*, oil globules in the central capsule; *c*, *d*, yellow cells; *e*, vacuoles.

in the central capsule (fig. 125), etc. In rare cases the skeleton is formed solely of organic substance (*acanthin*); usually it is silicious and of much firmness. Hence skeletons of Radiolaria occur in rocks of various ages, as in Caltanisetta, Sicily, the Nicobars (both tertiary), and the Barbadoes.

In reproduction first comes fission, which begins a division of the central capsule (in uni-nucleate forms with a division of the nucleus) and usually extends through the extracapsulum. If this latter does not divide a colony results, in which a gradually increasing jelly contains numerous central capsules, bound together by protoplasmic threads, which form the pseudopodia on the surface (fig. 126). A second type is reproduction by swarm spores, which begins when the nucleus has divided into hundreds or thousands of daughter nuclei. The central capsule then divides into as many portions as there are nuclei, which become oval and develop two flagella (fig. 127), which soon begin to vibrate so that the central capsule is filled with a tumultuous crowd. With the breaking of the capsular membrane these swarm spores escape, and at this point our knowledge of this type of development ceases. Since in many species there are large and small spores—macrospores and microspores—it is probable that for the further development a copulation of different swarm spores is necessary.

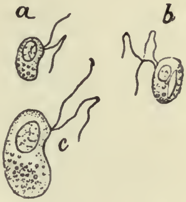


FIG. 127.—Zoospores of *Collozoum inerme*. *a*, microspore; *b*, zoospore with fusiform body; *c*, macrospore.

Common, if not constant, in the bodies of the Radiolaria are the yellow cells which were formerly regarded as a part of the animal; they are unicellular algæ (*Zooxanthellæ*), which are also present in other animals. (Thalamophora, actinians, sponges, etc.) They afford an instance of symbiosis, or the living together of different organisms for mutual good. This new view rests upon the facts that the *Zooxanthellæ* have a membrane, secrete starch-like substances, divide independently of the radiolarian and continue to live after its death.

The Radiolaria are exclusively marine. In fair weather they float at the surface, but sink in times of storm. Certain species and even large groups like the Phæodaria occur only at great depths (1500–4000 fathoms) where the temperature is about 0° C.

Sub Order I. PERIPYLEA or SPUMELLARIA. The capsule membrane everywhere perforated by pore canals; skeleton absent or formed of loose needles, of silicious latticed spheres, often reduced to a spongy network or flattened to discs. The latticed spheres can be provided with spines and connecting rods. SPHÆROZOIDÆ, colonial (fig. 126); THALASSI-

COLIDÆ (fig. 123); HALIOMMIDÆ with latticed spheres (fig. 85); DISCIDÆ, disc-like.

Sub Order II. ACANTHARIA. Capsular membrane perforated everywhere by pore canals; twenty spines of acanthin which radiate from the centre in an extremely regular manner, form the skeleton, as in *Acanthometra* (fig. 125), or the spines are bound together by a latticed sphere formed of twenty separate plates, as in *Acanthophracta*.

Sub Order III. MONOPYLEA or NASSELLARIA. The pores of the central capsule occupy a pore field at one end. Best known are the CYRTIDÆ (*Eucyrtidium*, fig. 124) with graceful helmet or cage-like skeletons.

Sub Order IV. PHÆODARIA. The central capsule has a principal opening, often drawn out into a tube and surrounded by dark pigment (phæodium) around which may be smaller openings. The skeleton is silicious and formed of hollow pieces. Mostly from the deep seas. *Aulacantha*, *Aulosphæra*, *Cœlodendron*, measuring from 0.5 to 1.0 mm., are pelagic.

Order V. Foraminifera (Thalamophora, Reticularia).

The Foraminifera, though not equalling the Radiolaria in beauty and variety of forms, excel them in numbers of individuals, and hence have a greater importance in the history of the earth. No group of animals at present or in the past have had so great a part in the formation of beds of rock.

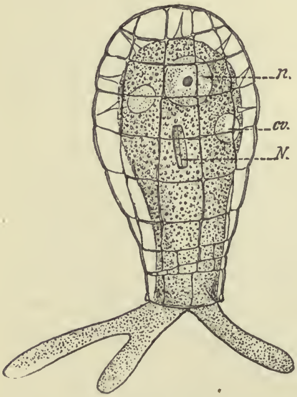


FIG. 128. — *Quadrula symmetrica*. (After F. E. Schulze.) *cv*, contractile vacuole; *n*, nucleus; *N*, food-body.

The most prominent characteristic of the order is afforded by the shell. This is an envelope, closed at one pole, and usually opening to the exterior at the other, the pseudopodia passing through the aperture (fig. 128). Accordingly as the axis connecting these poles is shortened or lengthened, the shell becomes disc-like, spherical, flask formed or even coiled in a spiral. An additionalfeature, the division of the interior of the shell by transverse partitions into numerous chambers, is common. Such many-chambered shells (Polythalamia) are at first small, and consist of one or few chambers, but as the animal grows new chambers are continually added at the mouth of the shell. Openings in the walls of the shell (*foramina*) connect the adjacent chambers. The spiral shells with many chambers have a striking resemblance to the much larger shells of the Nautilus (fig. 386), which led to the view once held that the Foraminifera were small cephalopods.

In the fresh-water forms the shell is built of a chitinuous organic substance which may be strengthened by silica or the incorporation of foreign particles. The more typical members, exclusively marine, have almost invariably calcareous shells which, when dissolved by acid, leave but the slightest trace of organic matter. The presence of minute pores in the shell is of systematic importance, the group of Perforata (fig. 117) being characterized by them.

The animal portions form a more or less complete cast of the inside of the shell (fig. 129), and in the polythalamate forms consist of as many pieces as there are chambers in the shell, connected together by plasma bridges passing through the foramina of the partitions. In the protoplasm there is a large nucleus (figs. 128, 129, *n*), which in some cases is early replaced by a daughter generation of small nuclei. Contractile vacuoles usually occur only in the fresh-water forms. The pseudopodia project through the chief opening of the shell and in the Perforata probably through the pores in the shell wall. They are rarely finger-like (fig. 128); usually they are thread-like, branched, richly granular and anastomosing, and hence favorable objects for the study of the streaming of protoplasm.

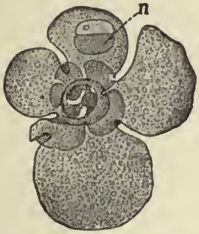


FIG. 129.—Protoplasm of *Globigerina* after solution of the shell. *n*, nucleus.

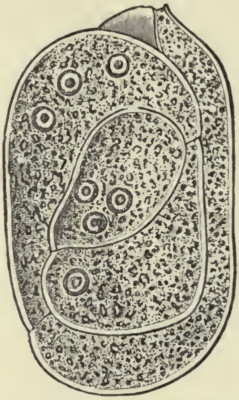


FIG. 130.—Young *Miliola* with several nuclei. (From Lang.)

Reproduction is generally accomplished by fission, but presents many variations. Only rarely do both animal and shell divide; frequently the protoplasm protrudes from the mouth of the shell, a new shell is formed on the outgrowth and the protoplasm then divides, one of the resulting individuals retaining the old shell. In the marine Polythalamia the following process is general: The polynucleate protoplasm divides into numerous uninucleate portions ('embryos') which frequently, while still within the mother, develop a shell of one or several chambers. In several species (*Polystomella crispa, Hyalopus dujardinii*, Miliolidæ, etc.) there is apparently a dimorphic alternation of generations. A megalospheric generation (characterized by the long persistence of a large 'principal nucleus,' and often of a large central chamber) produces zoospores. These develop into the microsphæric generation (early polynucleate, often with small central chamber), which form 'embryos' (*supra*), which in turn become megalospheres.

Sub Order I. MONOTHALAMIA. Mostly fresh-water forms. These species never have calcareous shells, but shells of chitin or silica, often strengthened by foreign bodies. Contractile vacuole usually present. Pseudopodia either lobose or filiform, branched or simple. *A.* Forms with finger-form pseudopodia: *Arcella*, brown disc-like shell, two or several nuclei; *Quadrula*, shell of many square plates (fig. 128); *Difflugia*, (fig. 131) with shells of sand. These forms may be regarded as merely shelled *Amœbæ* and are frequently referred to the Lobosa. All other Foraminifera are characterized by the filiform branching or anastomosing pseudopodia. *B.* Forms with branching and anastomosing filiform pseudopodia. *Euglypha*, shell of oval plates; *Gromia* (fig. 17), marine, shell a horny sac.

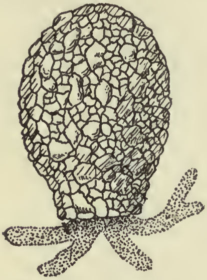


FIG. 131.—*Difflugia*. (Orig.)

Sub Order II. POLYTHALAMIA. Exclusively marine, living on aquatic plants, on the bottom or pelagic. The shells, when not dissolved, fall to the bottom in such numbers that a gram of the sand may contain 50,000 of them. Thick beds of rock like the chalk, the nummulitic limestone, and the greensand are largely foraminiferal in origin. The living species have an average diameter of about 1 mm. Rarely species have a diameter of several centimeters (*Psammonyx vulcanicus*, 5–6 cm.). The fossil nummulites reach a diameter of 6 cm. *A.* Shell wall massive, the terminal pseudopodal opening being the only communication with the exterior. *Miliola* (fig. 130). *B.* PERFORATA. Shell perforated by many pores; the terminal opening may be lacking. *Polystomella*, *Rotalia* (fig. 117), bottom dwelling; *Globigerina bulloides* (fig. 129), pelagic. Among the fossils the Nummulites need mention as well as the *Eozoon canadense* of the extremely old Laurentian beds of Canada, the animal nature of which is denied by most students.

Order VI. Mycetozoa.

The Mycetozoa or slime animals are regarded by some as animals, by others as plants under the older name Myxomycetes (slime moulds). The first position is supported by the structure of the motile stage, the plasmodium, the second by the reproduction resembling that of many fungi. The plasmodia appear in damp weather as networks of bright-red, orange or yellow slime on decaying wood. They are giant Amœbæ, several centimeters in extent, of reticulate protoplasm containing many nuclei and much foreign matter taken as food. They creep slowly by means of pseudopdia (fig. 132). On drying the plasmodium encysts in a peculiar manner, and if at the proper stage of maturity, it forms the reproductive bodies, the sporangia (fig. 133). These are firm-walled vesicles, frequently stalked, the stalk sometimes extending into the axis of the sporangium as a columella. The space between the wall of the sporangium and the columella is filled with fine powdery spores and an exploding apparatus, either a network of fine filaments (capillitium) or many spirally coiled threads (elaters). When wet, as by rain, the elaters or capillitium expand, rupture the sporangium and scatter the spores. The spores germinate in water or on moist surfaces, and from each comes out a small amœba-like embryo, frequently furnished with a flagellum (fig. 132). Several of these embryos fuse to form a plasmodium: *Æthalium septicum*, flowers of tan, plasmodium yellow, on spent tanbark; *Comatricha*, *Arcyria* (fig. 133).

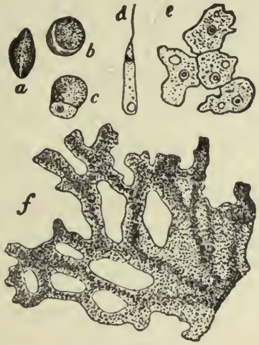


FIG. 132.

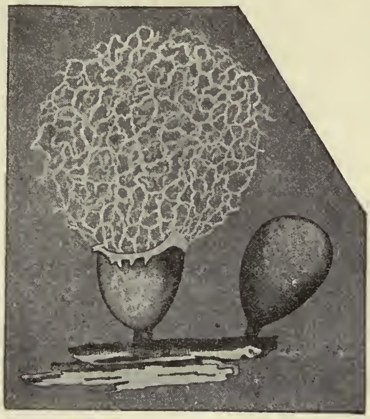


FIG. 133.

FIG. 132.—*Chondrioderma difforme.* (After Strasburger.) *a*, dry spore; *b*, swollen in water; *c*, spore with escaping contents; *d*, zoospore; *e*, amœboid modification of zoospores which are uniting to form a plasmodium; *f*, part of a plasmodium; in *d* and *e*, nuclei and contractile vacuoles.

FIG. 133.—Spore-sacs of *Arcyria incarnata.* (After de Bary.) At the left the sporangium ruptured by the expanding capillitium, which has discharged the spores.

Class II. Flagellata (Mastigophora).

In many Rhizopoda, as described in the foregoing pages, the pseudopodia disappear from time to time and are replaced by one or two flagella; others have, besides pseudopodia, permanent flagella for locomotion and taking of food. Such flagellate spores and flagellate Rhizopods form the transition to the Mastigophora, which are permanently flagellate, the flagella serving as organs of locomotion and feeding. There are three orders which must be described separately.

Order I. Autoflagellata.

All autoflagellates at first sight are closely similar, a usually oval body with a vesicular nucleus at one end, a contractile vacuole at the other. At the anterior end there is often added a small red or brown pigment spot (fig. 134), apparently for the recognition of light, and hence a primitive eye. At this same pole are also one or two flagella; when a greater number occur they are scattered over the body. The body surface is frequently naked, and may be capable of amœboid motions; at other times it is covered with a more or less evident cuticle. Very common are closed envelopes and open goblet-shaped cases (loricæ, fig. 135), and also simple or branched stalks (fig. 136), on which the animals

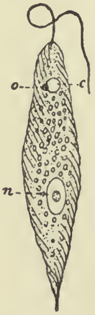


FIG. 134.

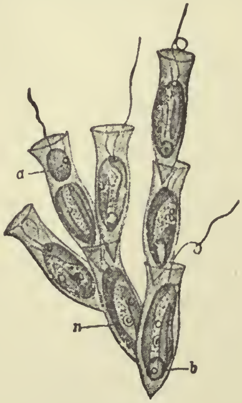


FIG. 135.

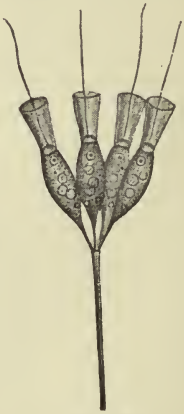


FIG. 136.

FIG. 134.—*Euglena viridis*. (After Stein.) *c*, contractile vacuole; *n*, nucleus; *o*, pigment spot.

FIG. 135.—*Dinobryon sertularia*. (After Stein.) *a*, a parasitic flagellate often found in the lorica; *b*, contractile vacuole; *n*, nucleus.

FIG. 136.—*Conocladium umbellatum*. (After Stein.)

sit in small groups. There are great differences in the feeding and in the organs connected therewith. Many feed like animals, being provided with pseudopodia like the Rhizopoda or with a mouth like the Infusoria. In the Choanoflagellata there is an interesting structure, the collar. This is a funnel-like process of the body protoplasm on which foreign particles are thrown by the flagellum in the centre (fig. 136) and thence are conveyed to the interior. (According to recent researches the collar consists of a plasma membrane rolled up spirally with two turns.) Besides these animal forms are plant-like species which contain chlorophyl (Volvocinæ, Euglenidæ) or brown chromatophores (Chromomonadineæ), aiding in assimilation and enabling the organism to produce paramylum or even starch. It is noteworthy that forms which are plant-like in this respect are closely allied anatomically to forms which resemble the animals. Indeed, there are species which possess a cytostome without taking solid nourishment, assimilating by means of chlorophyl or living on fluid food (fig. 137). All this renders more difficult the systematic valuation of the differences appearing in the food, and also shows that the Flagellata have relations in different directions: with the Rhizopoda, the Infusoria, and the lower plants.

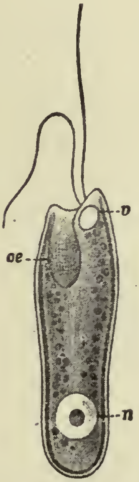


Fig. 137.

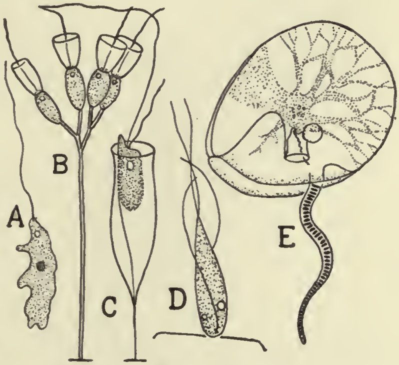


Fig. 138.

Fig. 137.—*Chilimonas paramœcium.* (After Bütschli.) *oe*, cytostome; *n*, nucleus; *v*, contractile vacuole.

Fig. 138.—Flagellata. *A*, *Mastigamœba*; *B*, *Codosiga*; *C*, *Bicoseca*; *D*, *Hexamita*; *E*, *Noctiluca*, side view.

Reproduction is nearly always by fission. In many species conjugation is known, best in those plant-like forms, the Volvocina, where two individuals fuse completely to a resting spore. In the colonial Volvocina the conjugating individuals are unequal in size, some animals of the colony growing to large immobile oospheres, while others by continued division form groups of minute active zoospores or spermatozoids. When fertilized by the zoospore the oospheres fall to the ground, become encysted, become brown in color, and enter a resting stage before they form a new colony by division.

Sub Order I. PHYTOFLAGELLATA. Plant-like chlorophyl-bearing flagellates, mostly with eye-specks. Volvocina: *Volvox globator*,* green sphere 0.2–0.7 mm. in diameter, consisting of thousands of individuals which propel the colony by their flagella. Euglenidæ : *Euglena viridis* * (fig. 134), solitary, coloring small pools bright green (a red variety colors them purple) by their immense numbers. Chrysomonadina, plant-like in nourishment but rarely taking solid food : *Dinobryon* * (fig. 136).

Sub Order II. CHOANOFLAGELLATA. With collars; mostly small colonial forms. *Codosiga* * (fig. 138, *B*) ; *Conocladium*, numerous individuals united on a stalk (fig. 136).

Sub Order III. EUFLAGELLATA. Animal flagellates, taking solid particles of food either by pseudopodia or by a more or less developed cytostome. Monadina. Here belong, besides numerous free forms, several parasites of man : *Lamblia* (*Cercomonas*) *intestinalis*, fig. 139 (*Megastoma entericum*); also in rats and mice : *Trichomonas hominis* (*T. intestinalis*), both in small intestine. *T. vaginalis* (fig. 140).

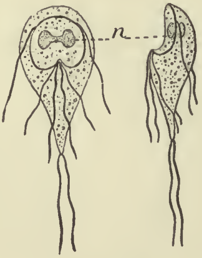


Fig. 139.

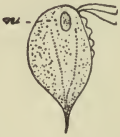


Fig. 140.

Fig. 139.—*Lamblia intestinalis.* (After Grassi.) Front and side views. *n*, nucleus.
Fig. 140.—*Trichomonas vaginalis.* (After Blochmann.) *n*, nucleus (fourth flagellum lacking in figure).

Order II. Dinoflagellata (Cilioflagellata).

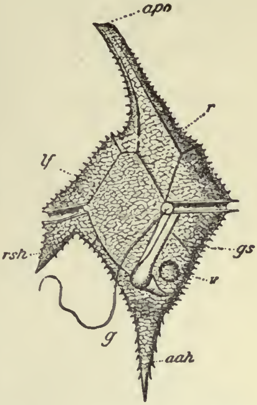


Fig. 141.—*Ceratium cornutum.* (After Stein.) *apo*, anterior horn with opening; *aah*, *rsh*, posterior and right horn; *g*, flagellum; *gs*, flagellar groove; *lf*, longitudinal groove; *r*, rhomboidal plate; *v*, vacuole.

These forms, occurring in both fresh water and the sea, are recently placed near the plants because, with their brown chromatophores, their food relations are like those of plants, although the taking of solid food by a mouth opening has been observed. The armor formed of cellulose plates is also plant-like. This armor is divided by a transverse groove into two parts which recall somewhat a box and its lid. There is also a longitudinal furrow which crosses the other. At the point of crossing are two flagella, one of which lies in the transverse groove and was for a long time regarded as a circle of cilia, whence the old name cilioflagellates given the order. *Peridinium tabulatum* and *Ceratium cornutum* (fig. 141); *Ceratium tripos,** marine.

Order III. Cystoflagellata.

The cystoflagellates, characterized by a gelatinous body surrounded by a membrane, include two very interesting species, both marine, which differ markedly in external appearance.

*Noctiluca miliaris** (figs. 142, 138, *E*), among all marine animals, best shows the phenomenon of phosphorescence. These spherical forms, about 1 mm. large, sometimes occur in such

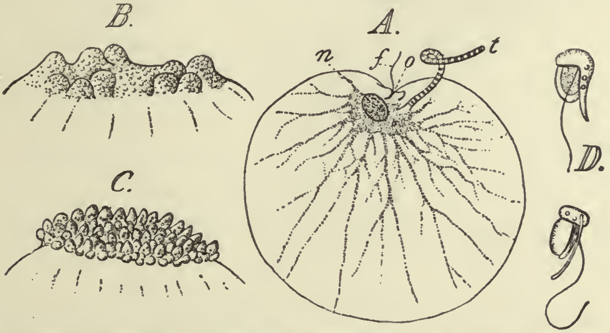


Fig. 142.—*Noctiluca miliaris* (in part after Cienkowski). *A*, entire animal; *f*, flagellum; *n*, nucleus; *o*, cytostome, beside it the 'tooth' and 'lip'; *t*, tentacle; *B*, *C*, upper end with two stages in the formation of zoospores; *D*, zoospores.

numbers at night as to make the whole surface light at the slightest agitation. The phosphorescence is apparently caused by oxidation processes in the protroplasm, but it persists for some time after deprivation of oxygen. The membrane covering the body is interrupted by a pit at one point, the cytostome, near which is the nucleus surrounded by an aggregation of protoplasm which sends branching threads into the jelly of the body. At the entrance to the cytostome is a flagellum, of no use in locomotion, and a band-like tentacle consisting of an outgrowth of the body membrane with a transversely banded muscular axis; it moves slowly with a swinging motion.

Noctiluca reproduces by simple fission and by formation of swarm spores (fig. 142, *B*, *C*, *D*). In the latter two individuals lose tentacles, flagella, and cytostomes, and conjugate; after mutual nuclear fertilization the animals separate, while the protoplasm in each collects in a disc which, by successive divisions, is converted into numerous uninucleate oval germs. These at first project from the sphere, but later separate and form small flagellate spores whose later history is not certainly known.

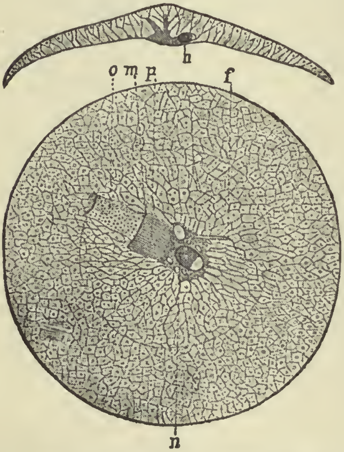


FIG. 143.—*Leptodiscus medusoides*, surface and optical section. *f*, flagellum; *m*, cytostome; *n*, nucleus; *o*, preoral tract; *p*, protoplasmic band.

Leptodiscus medusoides of Europe (fig. 143) has the appearance of a medusa 1 to 1.5 mm. in diameter. Its gelatinous disc is covered by a membrane, and at the highest point of the concave surface is a mass of protoplasm with a single nucleus. On one side of this a band goes to the mouth, on the other a canal bearing a fine flagellum at its end. The animals swim well, like medusæ, by closing the umbrella, the motions of which are caused by delicate muscles on the concave side.

Class III. Ciliata.

The Ciliata rival the Rhizopoda in numbers and variety of form. They are so complicated in structure that they were long held as multicellular, a view which was entirely abandoned only in the last quarter-century. All have a form definite for the species; this in the 'ametabolous' forms is unalterable, in the 'metabola' it can be pressed out of shape in passing through a narrow space. This constancy of form is due to the development of more or less cuticle on the outside of the body, which in the 'ametabola' acquires an armor-like firmness; in the others is more flexible. The cuticle is covered with cilia—small vibrating processes which move not singly but together in large numbers, and serve not only as organs of locomotion, but by creating vortices in the water bring food to the organism. They furnish the most important characteristic of the class (fig. 144).

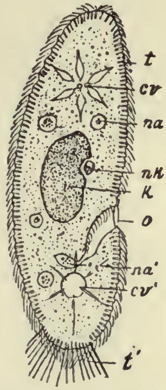


Fig. 144.—*Paramœcium caudatum* (half diagrammatic). *cv*, contractile vacuole in systole, *cv'*, in diastole; *k*, nucleus; *na*, food vacuole, *na'*, in formation; *nk*, micronucleus; *t*, trichocysts, at *t'* protruded.

The presence of a cuticle necessitates a cytostome (except in the parasitic species), since food particles cannot be taken in at any point. At the cytostome the cuticle with its cilia forms a funnel-like extension (cytopharynx) into the protoplasm. At the bottom the cuticle is interrupted so that water and protoplasm are in contact. By the action of the cilia food particles are taken into the cytopharynx and pressed into the protoplasm, forming a small enlargement which finally sinks into the substance as a food vacuole (*na*), which by the streaming of the protoplasm is carried about in the body. The digestible portions are absorbed, and those not capable of digestion are cast out of the body at a fixed point (cytopyge) usually not recognizable at other times (fig. 151).

Contractile vacuoles (*cv*) are lacking only in parasites and marine species. They are constant in number and position, and frequently have afferent ducts which empty into the vacuole, the vacuole in turn forcing the fluid to the exterior. Trichocysts, nettle bodies, and muscular fibrillæ occur in some species. Trichocysts are minute rods placed vertically to the surface in the cortical layer, which under the influence of reagents (chromic acid is best) elongate into threads penetrating the cuticula. These have been compared by some to the nettle cells of cœlenterates, and have been ascribed defensive functions; others regard them as tactile structures. They have no connexion with the cilia. Nettle bodies are extremely rare. Muscle fibres are more common; they lie between ectosarc and cuticle, and cause quick convulsive motions of the animal.

The nuclear relations are extremely interesting in that there are two nuclei physiologically unlike. The larger of these (nucleus of older writers, *macronucleus*) is a large oval, rod-like, or spiral body, readily and deeply staining with microscopic stains, and surrounded with a membrane. It appears to control all the common vital functions of the animal (motion, feeding, etc.). Beside it or in a depression in it is the much smaller *micronucleus* (nucleolus or paranucleus of older authors) which stains less deeply and only plays a part in reproduction. In all sexual processes it comes to the front and can be called the sexual nucleus.

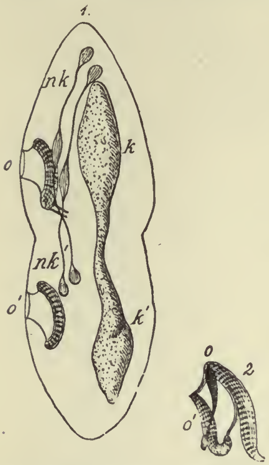


FIG. 145.—*Paramœcium aurelia* in division. *k*, macronucleus; *nk*, micronuclei; *o*, cytostome of the separating individuals. At *2* an early stage of division of cytostome.

Multiplication of Ciliata occurs by binary fission (fig. 145); more rarely, and then only in the encysted condition, by division into numerous (up to 64) parts. Budding is known in the Peritricha and Suctoria. First the micronucleus divides mitotically, and then the macronucleus separates by elongation and construction. The old cytostome persists in the anterior offspring, but often an outgrowth from it (fig. 145, *2*, *o'*) passes into the posterior half and develops into a new mouth.

The periods of fission are interrupted from time to time by the sexual process of conjugation, which will be described as it occurs in *Paramœcium* (fig. 146). Two individuals touch at first in front, and then by their whole ventral surfaces, so that their cytostomes come together. In the neighborhood of the latter a plasma bridge connects the two. Later the individuals separate. While these easily observable external processes are occurring there is a complete modification of the nuclear apparatus in the interior. The macronucleus increases in size, and breaks into small portions which disappear within the first week after copulation (probably absorption), and give place to a new nucleus derived from the micronucleus. At the beginning of copulation the micronucleus becomes spindle-shaped, divides and repeats the process, the result being the formation of four spindles, three of which break down, thus recalling the polar globules in the maturation of the egg (p. 146). The fourth or primary spindle places itself in the neighborhood of the cytostome at right angles to the surface and divides into two nuclei, the superficial being called the wandering or male nucleus, the deeper, the stationary or female nucleus. The male nuclei of the two copulating animals are exchanged, travers-

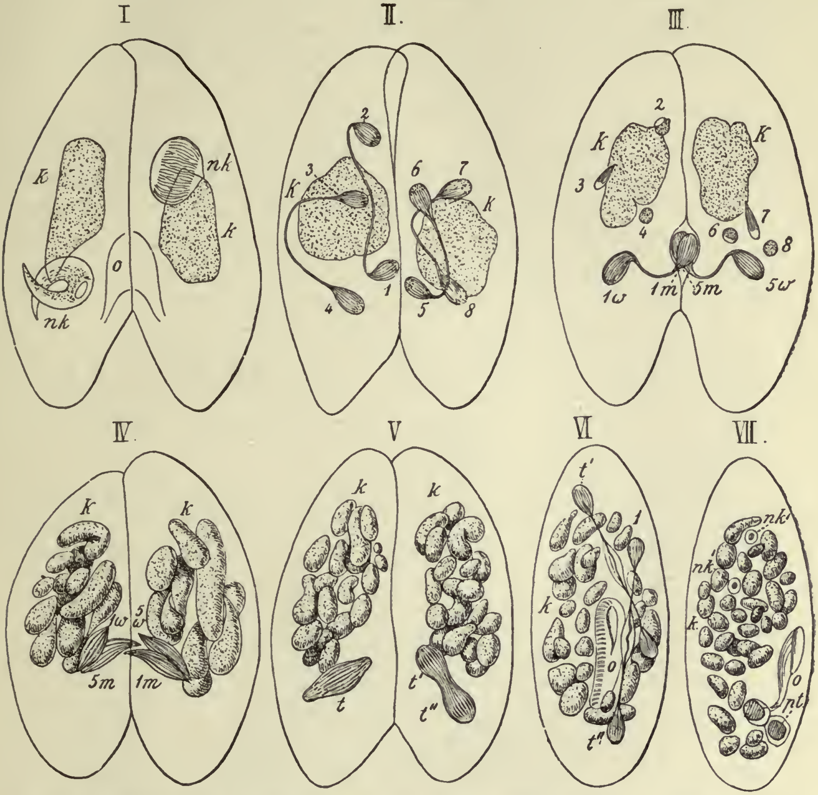


FIG. 146.—Conjugation in *Paramœcium*. *k*, macronucleus; *nk*, micronucleus; *o*, cytostomes.

I. Changes of micronucleus; left sickle stage, right spindle stage.

II. Second division of micronucleus into primary spindles (1, 5) and secondary spindles (2, 3, 4; 6, 7, 8).

III. Degeneration of secondary spindles (2, 3, 4; 6, 7, 8); division of primary spindle into male (1*m*, 5*m*) and female spindles (1*w*, 5*w*).

IV. Exchange of male spindles nearly complete (fertilization), one end still in the parent animal, the other united with the female spindle, 1*m* with 5*w* and 5*m* with 1*w*; macronucleus broken up.

V. The cleavage spindle *t* formed by male and female spindles dividing into the secondary cleavage spindles *t′*, *t″*.

VI, VII. End of conjugation. The secondary cleavage spindle dividing into the anlage of the new micronucleus (*nk′*), and that of the new macronucleus, *pt* (placenta). The fragments of the old macronucleus begin to degenerate.

Since *P. caudatum* shows the earlier and *P. aurelia* the later stages better, these forms have been used, *P. caudatum* for I-III, *P. aurelia* for the rest. The differences consist in the existence of one micronucleus in *P. caudatum*, two in *P. aurelia*, and that in the latter the nuclear degeneration begins in I.

ing the protoplasmic bridge in their course. Both male and female nuclei become spindle-shaped, and the immigrant male spindle fuses with the female spindle, forming a single spindle of division. At last the division spindle produces (usually by indirect means) two nuclei, one of which becomes the new macronucleus, the other the new micronucleus.

In a comparison of the fertilization of the Metazoa, the female nucleus corresponds to the egg nucleus, the male nucleus to that of the spermatozoa. As the fusion of egg and sperm nuclei forms a segmentation nucleus, so here the division nucleus is formed in a similar manner. As the egg cell through fertilization acquires the capacity not only to produce sex cells but somatic cells—cells which carry on the common functions of the body—the fertilized micronucleus forms not only the new micronucleus, but also the macronucleus which controls the body processes, and hence is the somatic nucleus. In other words, fertilization in the Ciliates leads to a complete new formation of the nucleus and thus to a new organization of the organism.

In most Ciliata the conjugating individuals are equivalent, the fertilization is mutual, and the individuals separate later. In the Peritricha (mostly sessile forms, fig. 147), on the contrary, the resemblance to fertilization in the Metazoa is strengthened in that there is a sexual differentiation and a permanent fusion of the conjugating individuals. Some animals—the macrospores—retain their size and sessile habits; others by rapid division produce

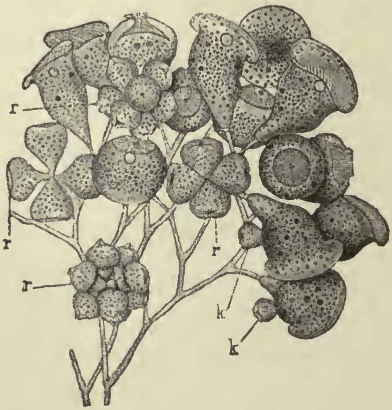


FIG. 147.—*Epistylis umbellaria.* (After Greeff.) Part of a colony in 'bud-like' conjugation *r*, microspores arising by division; *k*, microspore conjugating with a macrospore.

groups of markedly smaller microspores. The latter separate and fuse completely with the macrospores, only a small cuticular sac persisting to indicate the fusion. The nuclear phenomena are much the same as with *Paramœcium,* allowance being made for the permanance of the fusion.

Order I. Holotricha.

The Holotricha are doubtless the most primitive Ciliates, since the cilia on all parts of the body are similar; being at most slightly stronger at one end of the body or on the inside of the cytostome. Best known are the species of *Paramœcium* * (fig. 144) occurring in stagnant water. *Opalina ranarum* * lives in the intestine of the frog. It lacks mouth, has numerous similar nuclei, no micronucleus and no conjugation. The small encysted *Opalinæ* pass out with the fæces, and are eaten by the tadpoles, which thus become infected.

Order II. Heterotricha.

Like the Holotricha the Heterotricha are everywhere ciliated, but they have a tract of stronger cilia, the adoral ciliated spiral. This is a band of cilia beginning at some distance from the cytostome and leading in a spiral course into the mouth. It consists of rows of cilia united into 'membranellæ' placed at right angles to the course of the spiral. In the best-known heterotrichans, the *Stentors* * (fig. 148), the peristomial area, surrounded by

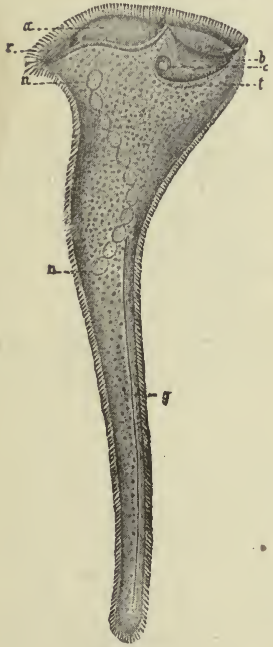


FIG. 148.

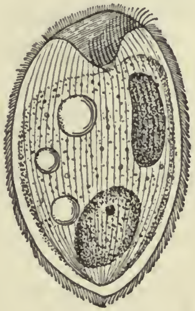


FIG. 149.

FIG. 148.—*Stentor polymorphus.* (After Stein.) *a*, peristomial area; *b*, roof of hypostome; *g*, contractile vacuole; *n*, nucleus; *o*, cytostome; *r*, adoral ciliated spiral; *t*, hypostome (excavation for mouth).
FIG. 149.—*Balantidium coli.* (After Leuckart.)

the spiral, forms the broader end of the body, which gradually tapers toward the other end, by which the animal may attach itself by small plasma threads. Muscle fibres which run lengthwise immediately under the cuticle produce energetic movements. *Stentor polymorphus** when attached builds a gelatinous case. *S. cœruleus.** *Balantidium coli* (fig. 149) appears in the large intestine of men ill with diarrhœa; it also occurs in swine without causing sickness. Other parasites of man are *B. minutum* and *Nyctotherus faba.*

Order III. Peritricha.

In the Peritricha there is always a broad peristome area with the cytostome; the opposite end has a corresponding pedal disc or is narrowed like a goblet and ends in a stalk (fig. 150). Only the adoral ciliated spiral is constant. It arises from the swollen margin of the peristomial area, and continues on the 'operculum,' a ciliated disc which projects free from the peristomial area, but in contraction is drawn close against it, the peristome lips folding over all. Besides, there may be a temporary or permanent circle of cilia near the hinder end. The nucleus is usually sausage-shaped, much bent, and with the small micronucleus in its hinder angle (fig. 150, *n′*).

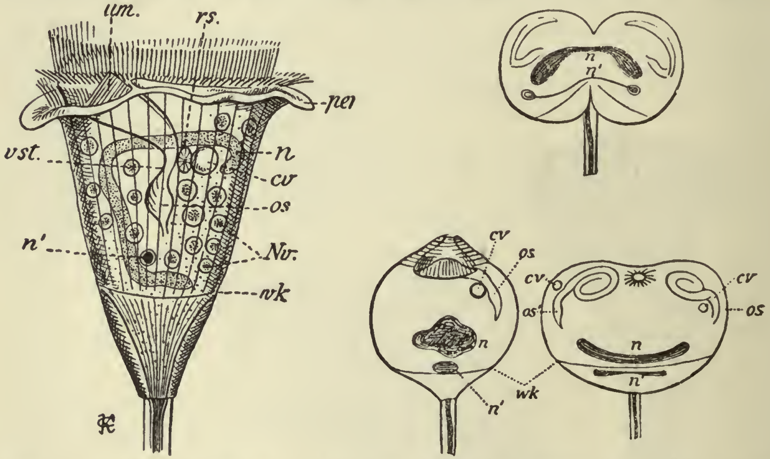


Fig. 150.—*Carchesium polypinum.* (After Bütschli.) Left, a single animal; right, three stages of division. *cv*, contractile vacuole; *n*, macronucleus; *n′*, micronucleus; *Nv*, food vacuoles; *os*, cytopharynx; *per*, peristome; *vs*, reservoir of contractile vacuole; *um*, undulating membrane; *vst*, vestibule; *wk*, ring on which a posterior circle of cilia may develop.

The best known representatives are the Vorticellidæ (figs. 147, 150), attached by a long stalk which is usually hollow and contains a slightly spiral muscle. This extends into the body and divides up into fine fibrillæ which extend under the cuticle to the peristome. When the muscle in the stalk contracts it becomes coiled into a corkscrew spiral, drawing back the animal, and folding in the anterior end. *Vorticella* * is solitary; *Carchesium* * forms colonies with dichotomously branched stalks; *Zoothamnion*,* colonies imbedded in a common jelly; *Epistylis* * (fig. 147), branched colonies with rigid stalks, the muscle being confined to the base of the body.

Order IV. Hypotricha.

In this order the body is more or less flattened and a ventral and a weakly arched dorsal surface are differentiated. The back lacks cilia, but often bears spines and tactile bristles. On the ventral side are several longitudinal rows of cilia, and besides straight spines and hooked cilia composed of united cilia. These latter are of use in creeping. The strongly developed adoral cilia are of use in locomotion and in producing vortices which bring food. The macronucleus is often divided into two oval bodies connected by a thread; the micronuclei vary in number from 2 to 4 in the same

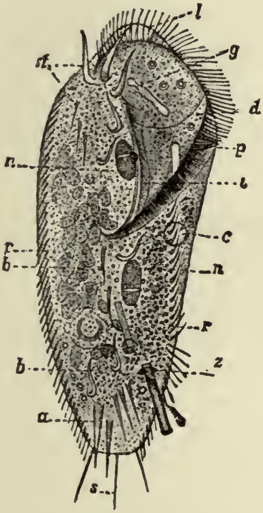


Fig. 151.

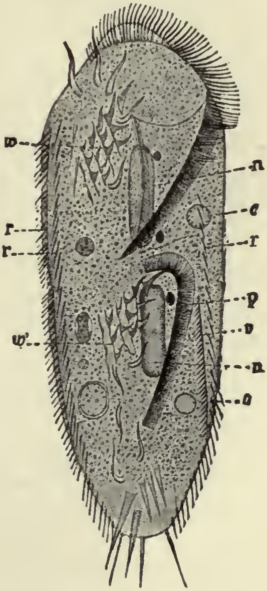


Fig 152.

Fig. 151.—*Stylonychia mytilus.* (After Stein.) *a*, anal hooks; *b*, ventral hooks; *c*, contractile vacuole; *d*, frontal ridge; *g*, canal leading to contractile vacuole; *l*, upper lip; *n*, nucleus with micronucleus; *p*, adoral ciliated spiral; *r*, marginal cilia; *s*, caudal cilia; *st*, frontal spines; *z*, anus (cytopyge).

Fig. 152.—Division of *Stylonychia mytilus.* (After Stein.) *c*, *c'*, contractile vacuoles of the two individuals; *n*, *n'*, nucleus and micronucleus; *p*, *p'*, adoral ciliated spiral; *r*, *r'*, marginal cilia; *w*, *w'*, ciliated ridges.

species. These are the best forms for studying the micronuclei. The species of *Stylonychia** (figs. 151, 152) are best known.

Order V. Suctoria (Acinetaria).

The Suctoria differ from other Infusoria in the absence of cilia from the adult and consequently have no means of locomotion. They are fixed to some support either by the base or by a slender stalk. The body is usually spherical and is covered with a cuticle, which in the genus Acineta is produced into a cup-like lorica. There is no mouth, but in its place tentacles or sucking feet, very fine tubes with contractile walls which begin in the protoplasm and protrude through the cuticle (fig. 153, *F*). The Acinetaria kill other animals, especially infusoria, with their tentacles, and then suck the substance through these tubes. The contractile vacuole, rarely lacking, lies near the compact macronucleus; micronuclei are generally present.

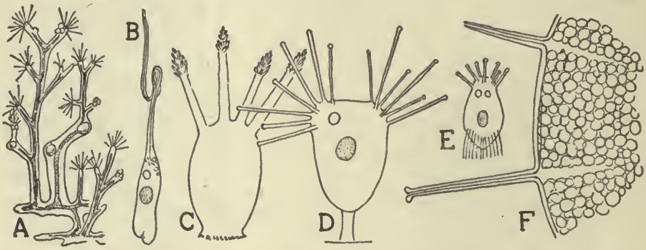


Fig. 153.—Forms of Suctoria. (After various writers.) *A*, *Dendrosoma;* *B*, *Rhyncheta;* *C*, *Ophryodendron;* *D*, *Tokophrya;* *E*, ciliated young of *Sphærophrya;* *F*, diagram of structure showing capitate and styliform tentacles arising from the ectosarc and corresponding canals in the entosarc.

In contrast to the immobile adults the young which are ciliated (fig. 153, *E*) after the pattern of ciliates, are good swimmers. They arise either as buds from the surface of the mother or as ‘embryos’ in her interior. This latter condition is only a modification of the other, for parts of the outer surface become pushed into the interior, and there form a brood cavity in which the embryos arise. After swimming for a while the young come to rest, lose the cilia, and develop the tentacles.

Some species of *Podophrya* are widely distributed in fresh water, also *Sphærophrya*, parasitic in Infusoria. The species of *Acineta* as well as *Podophrya gemmipara* (fig. 20) are marine, living on hydroids and Polyzoa.

Class IV. Sporozoa.

Under the name Sporozoa are united several groups of Protozoa which, while they differ much in structure, have much in common in life and development. They are parasites in Metazoa, many of them in the cells themselves, causing their degeneration (Cytosporidæ). They take no solid food, but are nourished by fluid material absorbed through the whole surface. In reproduction they form a large number of 'sporoblasts,' which when enveloped with a membrane are called 'spores,' the contents of which usually break up into several small bodies or 'sporozoites.' The sporozoites for their development must leave the host. The resemblances to the Rhizopods (Mycetozoa) are unmistakable, especially those Sporozoa which have pseudopodia for much of their life.

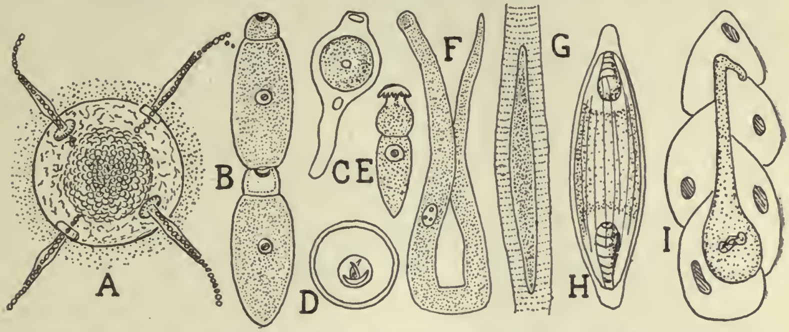


FIG. 154.—Sporozoa. *A*, cyst of *Clepsidrina* with sporoducts; *B*, *Clepsidrina*, two individuals (after Schneider); *C*, *Eimeria falciformis*, from mouse; *D*, same, falciform embryos; *E*, *Hoplorhynchus dujardinii*, from *Lithobius*; *F*, *Gregarina gigantea*, from lobster; *G*, *Sarcocystis miescheri*, from pig; *H*, *Myxidium* (after Théolan); *I*, *Rhopalocephalus*, alleged cause of cancer (after Korotneff).

Order I. Gregarina.

The typical and longest known sporozoa are the Gregarines, parasites of oval or thread-like form (recalling round worms), usually somewhat flattened, which so far have only been found in invertebrates, where they live in the intestine or gonads, more rarely in the body cavity. The protoplasm (fig. 155, *I*) is separated more sharply than in other Protozoa into a clear ectosarc (*ek*) and a granular entosarc (*en*). The ectosarc is covered by a cuticle (not always easily seen, but frequently with a double contour) (*cu*), which must be permeable by fluid food, for no cytostome exists. In many (perhaps all) there is a double striping of the body, a longitudinal recognizable by furrows on the outer surface and hence cuticular, and a transverse marking in the ectosarc, produced by circular or spiral muscle fibrillæ. These muscles explain the peristaltic motion and the occasional sharp bending of the body, but not the peculiar gliding motion like that of diatoms by which locomotion is usually effected. This is

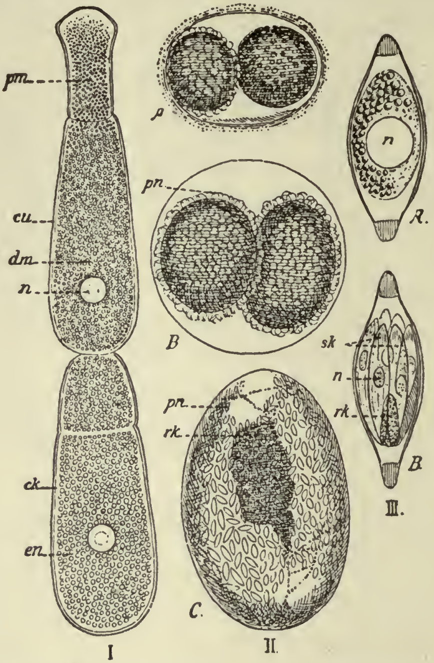


FIG. 155.—Development of *Gregarina blattarum*. I, conjugation; II, *A-C*, a cyst in transformation into pseudonavicellæ; III, *A*, a pseudonavicella greatly enlarged; *B*, same with sickle-formed sporozoites; *cu*, cuticle; *dm*, deutomerite; *ek*, ectosarc; *en*, entosarc; *n*, nucleus; *pm*, protomerite; *pn*, pseudonavicellæ; *rk*, residual body; *sk*, sickle-form sporozoites.

explained by the view that the gregarines secrete stiff gelatinous threads from the posterior end, and the elongation of these forces the body forward.

In many gregarines (Polycystidæ) the body is divided by a circular incision into a smaller anterior part, the protomerite, and a larger deutomerite. Internally this division is marked by a bridge of ectosarc across the entosarc. The vesicular nucleus (there is but one in any gregarine) lies in the deutomerite. An epimerite—a structure connected with the peculiar type of parasitism—occurs in many species. All gregarines are parasitic in youth inside of cells. They later leave these, but many remain for a long time with a process of the protomerite imbedded in the cells. This process—the epimerite—is provided with threads or hooks for anchorage, and is lost when the animal gives up its connexion with the host cell. Among the intestinal gregarines frequently occur 'associations' where two or more animals are fastened together head to tail in a row. Perhaps these associations are preparations for conjugation which occurs in development.

Reproduction occurs exclusively in an encysted condition (fig. 155, II, *A*). Usually two animals (sometimes one, rarely more than two) occur in a cyst. A fusion of the two encysted animals does not take place, but it is probable that a nuclear exchange (recalling that of ciliates) takes place. After each individual has become polynucleate by division of its nucleus, it divides at first superficially, later internally into small particles, the sporoblasts (II, *B*), which change into spores, here called pseudonavicellæ. The pseudonavicellæ are mononucleate bodies with firm membrane and usually spindle form in shape (III, *AA*). In these processes a part of the gregarine takes no part. This residual body appears under proper conditions to swell up and rupture the cyst, thus freeing the pseudonavicellæ. In many gregarines there are sporoducts for the escape of the pseudonavicellæ (fig. 154, *A*). The contents of the pseudonavicellæ divides into (usually eight) sporozoites or falciform spores which must pass out from the spores and into the cells of the host in order to form gregarines. This escape of the sporozoites depends upon entrance into the proper host. Often the transformation of the contents of the cysts into pseudonavicellæ takes place when the cysts have left the original host.

Best known are the *Monocystis tenax* of the spermatheca of earthworms, and *Gregarina* (*Clepsidrina*) *blattarum* of the cockroach. The American species have scarcely been touched. One species is abundant in the intestine of *Geophilus*.

Order II. Coccidiæ.

The gregarines of all Sporozoa are nearest the Coccidiæ, which are also cell parasites with a single nucleus, but without either cell membrane or division into protomerite and deutomerite. In most species, as in *Coccidium cuniculi*, there are two types of reproduction, an endogenous, leading to 'autoinfection,' and an exogenous, concerned in the transfer of the germs to other hosts. In the first (lacking in many species) the *Coccidium* divides into many falciform germs which separate from each other and, without alternation of hosts, enter other cells. The second type is begun by fertilization. Certain individuals, by rapid division form microgametes, small bodies swimming with serpentine motions or by one or two flagella. Other individuals do not divide, but form macrogametes which are fertilized by the microgametes, and then encyst, pass to the outside, and serve for the infection of other animals. The contents of the cyst begin to divide, sooner or later, into sporoblasts (in *Coccidium*, four) containing spores, the process being completed only after entrance into a new host. Each spore forms one or more sporozoites, a portion of the substance being left behind. *Coccidium cuniculi* (*oviforme*) in the liver of mammals, especially rabbits (rare in man), producing cheesy granules. *C. perforans* in the intestine of rabbits, rare in man.

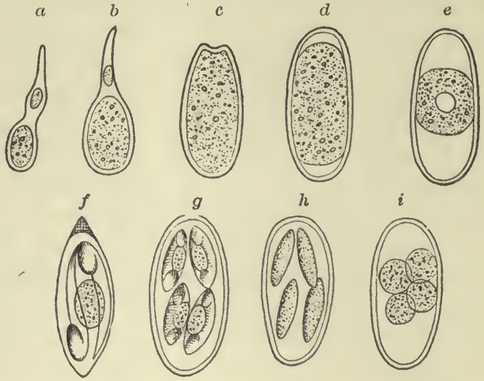


Fig. 156.—*Coccidium cuniculi*, from the liver of the rabbit (from Wasielewski. *a*, *b*, young *Coccidia* in the epithelial cells of bile duct, the nucleus of the cell in the upper process; *c*, encysted; *d*, *e*, contraction of protoplasm; *i*, *h*, *g*, spore formation; *f*, ripe spore with two germs and a residual body.

Order III. Hæmosporida.

In structure and development these are much like the Coccidiæ; they live in blood corpuscles. The forms occurring in man produce malaria. Here, also, there are endogenous (autoinfecting) and exogenous generations transferring the parasites to other hosts. The parasites in the corpuscles (fig. 157, *a* to *d*) grow and divide, producing 'daisy-like forms' characterized by little accumulations of pigment derived from the hæmoglobin of the blood.

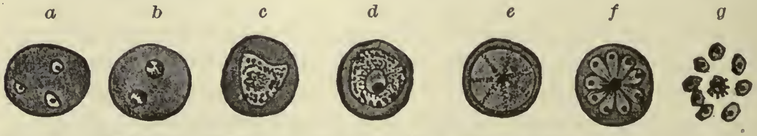


Fig. 157.—*Plasmodium laverni*, var. *quartana* (from Wasielewski, after Labbé), from the blood of a malarial man. *a*, newly infected blood corpuscle; *b*, somewhat larger germs; *c*, full-grown parasite with strong pigmentation; *d*, rounded form with large nucleus; *e*, beginning of germ formation; *f*, rosette of germs around a residual body; *g*, germs set free by degeneration of corpuscle.

These division products are set free by a breaking down of the corpuscle (period of chill) and infect other corpuscles. Thus autoinfection can continue until at length sexual forms appear—'spheres' or macrogametes, flagellate microgametes—incapable of infecting the corpuscles. The conjugation of these seems to take place when they are taken into the stomach of a blood-sucking mosquito. After fertilization, the oosphere wanders into the intestinal wall of the mosquito, grows larger, encysts, and produces many sporoblasts, which in time form many sporozoites. These migrate into the salivary glands of the mosquito and thence are transferred to man with the sting of these insects. Since a temperature above 20° C. (68° F.) is best for the development of the stages in the mosquito, and since mosquitos need water for their development, the prevalence of the disease in moist, warm regions is easily understood. For the transfer of human malaria not all mosquitos will serve, but apparently only those of the genus *Anopheles*. The species of *Culex* convey bird malaria. The different kinds of malaria seem to be produced by different parasites.

Order IV. Myxosporida.

The Myxosporida (fig. 158) are mostly large (sometimes visible to the naked eye) and occur especially in fish and arthropods. When they occur in hollow organs they are naked and have pseudopodia, but in parenchymatous organs like the heart, liver, brain, kidney, etc., they are usually enclosed in a membrane, and here they produce the greatest injury. At first binucleate, they soon become polynucleate, and it would appear that they can reproduce by fission. Even before the growth is ended they begin the process of sporulation. In the interior single spherical protoplasmic bodies separate, these having at first a single nucleus, later more (as many as ten). From each of these bodies arise from two to many spores, the so-called psorosperms. These (fig. 158, *3*) are enclosed in a bivalve shell which includes, besides a binucleate germ, one, two, or four polar capsules, these resembling somewhat the nettle organs of the cœlenterates. They are oval and contain threads which, under certain conditions, are protruded (fig. 158, *2*)

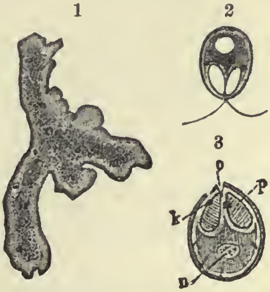


FIG. 158.—Myxosporida. 1, *Myxobolus mülleri*, from gills of a fish; *2*, *3*, psorosperms of *Myxidium lieberkuhni*; *k*, degenerating nucleus; *n*, vacuole formerly regarded as a nucleus; *p*, cnidocil-like pole body, in *2* with exserted threads.

and serve to fix the capsule, while the amœboid germ creeps out and penetrates the tissues of the host. Experiment shows that fishes are infected through the alimentary canal.

The Myxosporida frequently cause serious epidemics in fish. This was noticeably the case with the fish in the aquaria at the Chicago exposition. *Myxobolus*, *Myxidium*. Invertebrates may also be infected, the celebrated pébrine of the silkworm being caused by *Nosema* (*Glugea*) *bombycis*.

Order V. Sarcosporida.

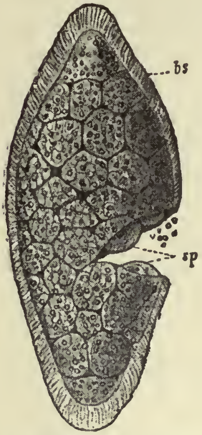


FIG. 159. — *Sarcocystis miescheriana*, from diaphragm of pig. (After Bütschli.) *bs*, cyst; *sp*, spheres of spores.

The Sarcosporida (fig. 159)—also called Rainey's or Miescher's corpuscles—occur in the voluntary muscles of vertebrates, especially mammals. They are oval cysts lying in sarcolemma sacs between the fibrillæ. They have a cyst, the wall of which is radially striped, and inside this, in the ripe condition, are spores, imbedded in a stroma, each spore containing numerous reniform or falciform sporozoites. *Sarcocystis miescheriana* in muscles of pig; *S. muris* in the mouse; *S. lindemanni* rare in human muscle.

Summary of Important Facts.

1. The Protozoa are unicellular organisms without true organs or true tissues.

2. All vital processes are accomplished by the protoplasm (sarcode), digestion directly by its substance, locomotion and the taking of food by means of protoplasmic processes (pseudopodia) or by appendages (cilia and flagella).

3. Excretion takes place by special accumulations of fluid, the contractile vacuoles.

4. Reproduction is by budding or by fission. Conjugation has been witnessed in many, and possibly occurs in all. True conjugation is a process of fertilization (caryogamy), in contrast to fusion of plasma (plasmogamy).

5. Protozoa are aquatic, a few living in moist earth; they can only exist in dry air in the encysted condition, surrounded by a capsule which prevents desiccation.

6. Since encysted Protozoa are easily carried by the wind, the occurrence of these animals in water which originally contained none is easily explained.

7. The mode of locomotion serves as the basis for division of

the Protozoa into the classes Rhizopoda, Flagellata, Ciliata, and Sporozoa.

8. The Rhizopoda have changeable protoplasmic processes, the pseudopodia.

9. The Rhizopoda are subdivided into Monera, Lobosa, Heliozoa, Radiolaria, Foraminifera, and Mycetozoa.

10. The *Lobosa* and *Monera* have no definite shape. The Lobosa have a nucleus, the Monera are anucleate.

11. *Heliozoa* and *Radiolaria* are spherical and have fine radiating pseudopodia and frequently silicious skeletons. They are distinguished by the occurrence of a central capsule in the Radiolaria which is lacking in the Heliozoa.

12. The *Thalamophora* (Foraminifera) have a shell, closed at one end, at the other with opening for the extension of pseudopodia. The shell is chitinous or calcareous, one or several chambered, straight or spiral, sometimes with close walls, sometimes perforated with pores; the pseudopodia are occasionally lobular, but usually filiform, branching and anastomosing.

13. The Foraminifera are of great geological importance on account of their numbers and their shells, which have built and are still building extensive beds of rock (chalk, nummulitic limestone). The silicious skeletons of the Radiolaria are less important.

14. *Mycetozoa* (Myxomycetes of botanists) are mostly enormous Amœbæ with branched reticulate protoplasm (plasmodium). They form complex reproductive structures (sporangia, etc.), recalling those of the fungi.

15. Flagellata have one or a few long vibratile processes—flagella—which serve for locomotion and for the taking of food.

16. The *Autoflagellata* have only flagella; they feed like plants (Volvocina) by means of chlorophyl, or have a mouth for the taking of food, or a collar (Choanoflagellata).

17. The *Dinoflagellata* have two kinds of flagella and usually an armor of cellulose.

18. The *Cystoflagellata* have a gelatinous body enclosed in a firm membrane (*Noctiluca*).

19. The Ciliata (Infusoria in the narrower sense) have numerous slender vibrating processes, the cilia, a cuticle, and hence fixed openings for the ingestion of food (cytostome) and for extrusion of indigestible matter (cytopyge).

21. Of great interest is the occurrence of two kinds of nuclei, a functional nucleus (macronucleus) and a sexual nucleus (micronucleus, paranucleus).

22. In conjugation portions of the micronucleus are exchanged and accomplish impregnation. The macronucleus degenerates and is replaced by part of the fecundated micronucleus.

22. The classification of the Ciliata is based on the structure and arrangement of the cilia.

23. The *Holotricha* have similar cilia over the whole body. The *Heterotricha* have besides the total ciliation stronger cilia in the neighborhood of the mouth (adoral ciliary spiral). The *Peritricha* have only adoral ciliation. The *Hypotricha* have, on the ventral surface, the ciliary spiral and rows of cilia and coalesced cilia. The *Suctoria* have cilia only in the young, later they become attached and feed through suctorial tentacles.

24. SPOROZOA are parasitic Protozoa, usually without organs of locomotion or mouth. They take no solid food, but live by osmosis on tissue fluids. In reproduction the encysted animals produce spores (apparently always beginning with fecundation and accompanied by a change of host). The spores divide again into sporozoites. Besides, multiplication without change of host (auto-infection) can occur.

25. The *Gregarinida* are temporary or permanent parasites in cells. (Spores = pseudonavicellæ, sporozoite = falciform embryo). *Coccidiæ*, *Hæmosporida* (cause of malaria, parasitic in blood corpuscles).

26. The *Sarcosporida* (Rainey's or Miescher's corpuscles of mammalian muscles) and *Myxosporida* (psorosperm capsules of fishes, psorosperm = spore) live in tissues or hollow organs.

APPENDIX.

According to the evolution theory one should expect forms between the Protozoa and Metazoa. The CATALLACTA—spheres of ciliated cells which in reproduction break up into single cells—have been described as such.

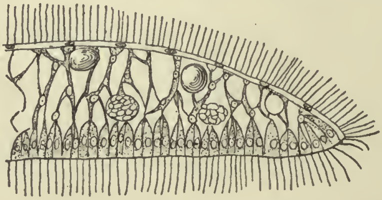


FIG. 160.—Section of half of *Trichoplax adhærens*. (After Schulze.)

Peculiar many-celled animals whose position in the system is difficult to decide are, further, *Trichoplax adhærens*, *Salinella salve*, the ORTHONECTIDA and the DICYEMIDA. *Trichoplax* (fig. 160) is discoid and consists of two epithelial-like cell layers separated by gelatinous tissue. The Orthonectida and Dicyemida have a many-celled ectoderm, enclosing a solid mass of cells in the Orthonectida, a single giant cell in the Dicyemida. *Salinella* consists of a single layer of cells enclosing a central digestive space. Since the Dicyemida live as parasites in the nephridia of cephalopods, the Orthonectida in worms and echinoderms, it is possible that their low organization is the result of degeneration.

METAZOA.

Excluding the Protozoa, all the branches of the animal kingdom may be included under the head Metazoa, i.e. higher animals. The point of union is that they consist of numerous distinct cells, and that these cells are arranged in several layers. At least two layers are present, a layer—the ectoderm—which bounds the body externally, and a second, lining the digestive tract—the entoderm. Between these two a third layer can occur, which frequently is separated by a body cavity into an outer or somatic layer forming part of the body wall, and an inner or splanchnic layer forming part of the intestinal wall. This middle layer is called mesoderm no matter whether there be a body cavity or not.

The multicellular condition allows a higher development of the organization, which appears in varying grades in the specialization of tissues and organs. In no metazoan is there lacking a true sexual reproduction, that is one by sexual cells, but the fact must not be overlooked that many species reproduce (possibly exclusively) by unfertilized eggs in a parthenogenetic manner. Besides the sexual reproduction many species, especially the lower worms and cœlenterates, reproduce by budding and fission.

For all the Metazoa the segmentation of the egg is characteristic to a high degree. The fecundated egg divides into numerous cells which, as segmentation cells (blastomeres), remain united and form the germ. No Protozoan has a true segmentation. Division there produces new individuals which either separate completely or exceptionally remain in slight connexion as a colony.

PHYLUM II. PORIFERA (SPONGIDA).

The Porifera, or sponges, the most familiar representative of which is the bath sponge (*Euspongia officinalis*), are, with few exceptions, marine. In fresh water occur but a few species of *Spongilla* (recently subdivided into several subgenera). The animals have no powers of locomotion, but are attached to stones or plants, along the shores or at depths up to 6000 metres (4000 fathoms). They form spherical masses, thin crusts, small cylinders, or upright branching forms. Frequently the shape varies so that one cannot speak of a typical form. It was also difficult to decide about the animal nature of the sponges. Striking movements of the body are rare; only by aid of the microscope can one see motion—the opening and closing of the pores and the streaming of the gastrovascular system.

The simplest sponges, the Ascons (fig. 161), are thin-walled sacs, fixed at one end, and with an opening, the osculum (functional anus), at the other. The cavity of the sac, the 'stomach,' is a wide digestive cavity into which water bearing food obtains entrance through numerous small openings or pores in the body wall. The basis of the body is a homogeneous or fibrous connective tissue permeated with branching cells (fig. 162) covered externally by a thin layer of pavement epithelium which is easily destroyed. This epithelium (earlier called ectoderm) and the connective tissue (mesoderm) are now regarded as a common layer, 'meso-ectoderm,' since it has been shown that the pavement epithelium is often genetically only connective-tissue cells which have spread over the surface. On the other hand there is a distinctly differentiated entoderm in the shape of a one-layered flagellate epithelium lining the stomach, the cells of which (*en*) recall the Choanoflagellata

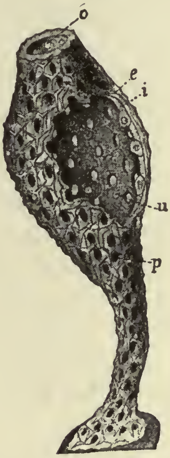


FIG. 161.

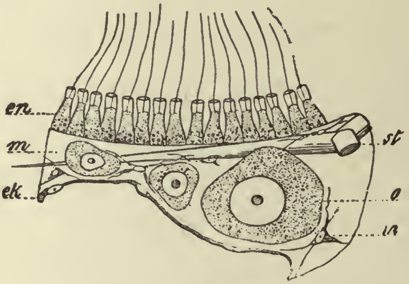


FIG. 162.

FIG. 161.—*Olynthus.* (After Haeckel.) *e*, spicules; *i*, eggs; *o*, osculum; *p*, pores; *u*, 'stomach.'

FIG. 162.—Section of wall of *Sycandra raphanus.* (After Schulze.) *e*, ectodermal epithelium; *en*, collared flagellate cells; *m*, mesoderm with connective-tissue cells; *o*, eggs; *st*, calcareous spicules.

(p. 202), since they have collars surrounding the flagella. It has therefore been attempted to regard each flagellate cell as an individual, and the whole sponge as a colony of Flagellata, a view which neglects the other tissues, not only the connective tissue and the epithelium already mentioned, but sex cells, amœboid wandering cells, and contractile fibre cells which close the pores. The taking of food is accomplished by the collared cells.

Sponges of this simple ascon type are few. As a rule the sponges are more massive and have a more complicated canal system (figs. 164–166). The first step towards complication is seen in the Sycon sponges (fig. 163), in which the gastral cavity consists of numerous radial outpushings (the flagellate chambers or ampullæ) which alone contain the collared cells, while the central cavity, now called cloaca, is here lined with pavement epithelium. By increase of mesoderm and corresponding thickening of the body wall the ampullæ become separated from external and cloacal surfaces by the ingrowth of tissue (Leucon type). The ampullæ nevertheless retain their connexion with both surfaces by means of a system of canals. This canal system is double; one part is incurrent and leads from the dermal pores to the ampullæ;

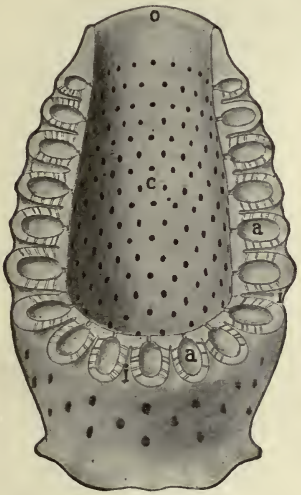


FIG. 163.

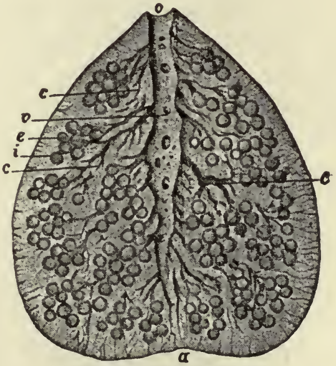


FIG. 164.

FIG. 163.—Stereogram of Sycon sponge (orig.). *a*, ampullæ with pores in their walls; *c*, cloacal chamber, with the openings of excurrent canals; *i*, incurrent canals; *o*, osculum.

FIG. 164.—Section of *Leucortis pulvinar*. (After Haeckel.) *a*, aboral pole; *c*, efferent canals from the ampullæ to the cloaca; *e*, ampullæ; *i*, mesoderm; *o*, osculum; *v*, cloaca.

the other or excurrent from the ampullæ to the cloaca, the two being connected by the ampullæ alone. Both may consist of lacunar spaces (fig. 164), or have a more regular arrangement (fig. 165), the canals from the pores uniting in trunks and these in turn branching to go to the ampullæ. The excurrent canals also show a similar tree-like arrangement. Not infrequently extensive subdermal or subcloacal spaces occur. The relations may be more complicated by the development of several cloacæ, or these may be repressed; again by the branching of the sponge (fig. 167), while still further the branches may anastomose (fig. 168), giving rise to a network.

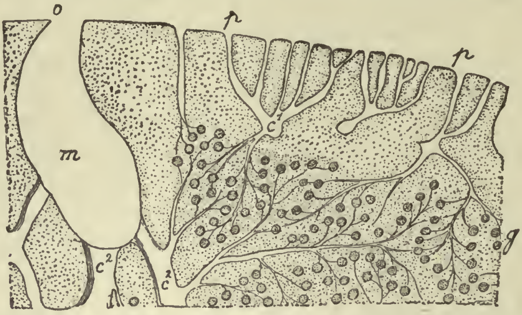


FIG. 165.—Section of cortex of *Chondrilla nucula*, the skeleton omitted. (After Schulze.) c^1, afferent canals; c^2, efferent canals; *g*, ampullæ; *m*, cloaca; *o*, osculum.

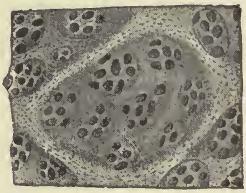


FIG. 166.

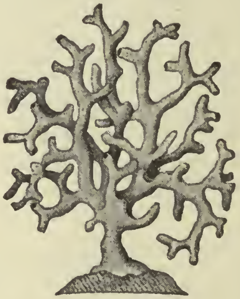


FIG. 167.

FIG. 166.—Surface view of dermal pores of *Aplysina aërophobia*. (After Schulze.)
FIG. 167.—*Ascyssa acufera*. (After Haeckel.)

Sponges may reproduce asexually, small portions separating as buds and producing new animals. Usually sexual reproduction prevails. Eggs and spermatozoa arise from mesoderm cells (fig. 162), are fertilized and undergo segmentation at the point of origin, and leave the parent as flagellate larvæ (fig. 169, *A*). At fixation a kind of gastrulation takes place, the blastopore (fig. 169, *B*) closes, and the osculum, an entirely new formation, arises at the opposite pole.

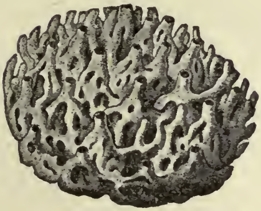


FIG. 168.

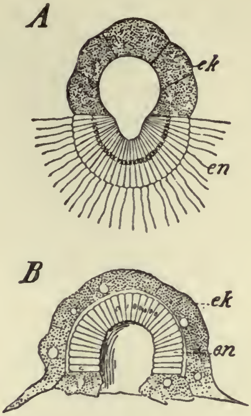


FIG. 169.

FIG. 168.—*Leucetta sagittata.* (After Haeckel.)
FIG. 169.—Development of *Sycandra raphanus.* (After Schulze.) *A*, blastula; *B*, gastrula at the moment of fixation; *ek*, ectomesoderm; *en*, entoderm.

The sponges are frequently regarded as Cœlenterata, but scarcely a single homology can be drawn between the two. The cœlenterate mouth is different from either pores or oscula. Indeed it is disputed whether the collared cells are entoderm. Nearly all sponges possess a skeleton secreted by special mesoderm cells, and this skeleton affords the means, according as it is composed of calcic carbonate or of silica, of dividing the sponges into two classes. Besides, there are two groups, the Ceraospongiæ and the Myxospongiæ, in which the skeleton is respectively of horny substance or spongin or is lacking entirely. These, however, seem to be descendants of the silicious forms.

Order I. Calcispongiæ.

The calc sponges are exclusively marine and mostly live in shallow water. They are grayish or white in color, of small size, rarely exceeding an inch or so in length. The skeletal spicules which arise in the mesoderm usually project through the epithelium and form, especially in the neighborhood of the osculum, silky crowns. One-, three-, and four-rayed spicules are recognized, these ground forms presenting by unequal development a great variety of shapes (fig. 170).

Sub Order I. ASCONES. Sponges with thin porose walls and a central 'stomach' (figs. 161, 167). *Leucosolenia.**

Sub Order II. SYCONES. A cloaca present surrounded by ampullæ radially arranged (fig. 163). *Grantia,* Sycon,* Sycandra.**

Sub Order III. LEUCONES. A complicated system of branching incurrent and excurrent canals in the thick walls connects the ampullæ with the outer surface and the cloacal cavity (figs. 164, 168). *Leucetta, Leucortis.*

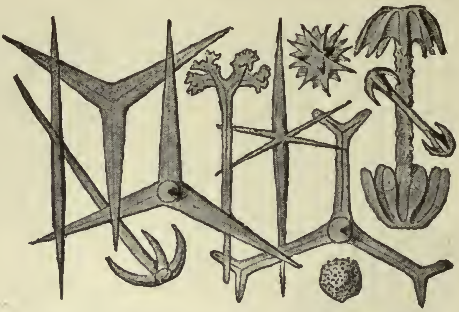


Fig. 170.—Sponge spicules. (From Lang.)

Order II. Silicispongiæ.

The siliceous sponges are richest in species and occur at all depths of the sea, being frequently noticeable from their size (up to a yard) and their bright colors. They are subdivided into Triaxonia and Tetraxonia. In the Triaxonia the spicules composing the skeleton—appearing as if of spun glass (hence Hyalospongia, or glass sponges)—have three crossed axes (six threads radiating from a common point)—hence Hexactinellidæ. The mesoderm is scanty and in consequence the afferent and efferent canals are loose-meshed lacunar spaces and the ampullæ large and barrel-formed. In the Tetraxonia, on the other hand, the mesoderm is usually abundant and the canal system well developed. The four-axial spicules of the Tetractinellidæ must be regarded as the fundamental skeletal type. From this are derived the compact agglutinated frameworks of the Lithistidæ and the monaxial spicules of the Monactinellidæ.

In both groups the spicules may be united by secondary deposits of silica to an extensive framework; or the union is effected by spongin, which, if the spicules disappear, forms the whole skeleton (horny sponges), or, as in slime-sponges, the whole skeleton may be lost.

Sub Order I. TRIAXONIA. The HEXACTINELLIDÆ belonging here live chiefly in the deep sea, and for a long time only a few species were known: *Euplectella aspergillum*, Venus' flower-basket, tubular, consisting of fine spicules. *Hyalonema.* 'Apparently the horny sponges *Aplysina* and *Aplysilla*, as well as the slime-sponges, *Halisarca*,* have descended from this group.

Sub Order II. TETRAXONIA. Typical representatives are the largely extinct LITHISTIDÆ (of which some genera—*Discodermia*—persist in deep seas) and the TETRACTINELLIDÆ: *Geodia.** Near here apparently belongs *Oscarella,** without a skeleton (Myxospongia).

In the MONACTINELLIDÆ the spicules are united by spongin (Cornacuspongia), and can even be entirely replaced by that substance. Numerous marine forms, among them *Chalina,** and also the fresh-water SPONGILLIDÆ (*Spongilla,* *Ephydatia* *), widely distributed as encrusting masses on submerged sticks and stones. The natural color is light gray, but they are usually colored green by Algæ. They are distinguished from most marine relatives by the formation of gemmulæ or statoblasts. At times the protoplasm divides into round bodies, as large as the head of a pin and these become surrounded by a firm membrane strengthened in many forms by collar-button-like spicules, the amphidiscs. These statoblasts remain entangled in the skeleton and survive times of freezing or drought. On return of good conditions the contents escape and form small *Spongillæ*, often utilizing the old skeleton. This process recalls encystment among the Protozoa.

When the spicules entirely disappear and nothing but the spongin fibres remain we have the horny sponges or CERAOSPONGIÆ. The skeleton consists of a horny substance, spongin, which differs chemically from the substances of true horn—keratin. This spongin is always laid down in long fibres by peculiar cells, the spongioblasts, and it always consists of concentric layers. The fibres interlace, branch, and unite into a skeleton.

The best known horny sponges are the bath sponges, *Euspongia officinalis,** occurring in the Mediterranean, West Indies, Florida, and other seas in many varieties. Best of all are the Levant sponges (var. *mollissima*). Sponges of commerce consist only of the skeleton, the animal parts being killed and, after decay, washed away with fresh water. Less valuable are *Euspongia zimocca* and *Hippospongia equina,** the horse-sponge, while the *Cacospongiæ* are useless.

Summary of Important Facts.

1. The sponge body is largely a mass of connective tissue covered externally with pavement epithelium (meso-ectoderm) and penetrated by canals.

2. An entoderm of collared flagellate cells occurs only in the ampullæ or flagellate chambers which are intercalated between incurrent and excurrent canals (in ascons in the central cavity).

3. The animals receive nourishment through fine pores in the body wall; indigestible bodies are cast out through one or several oscula.

4. Since nerves, muscles, and sense organs are lacking or very weakly developed, the animals show the most inconspicuous movements.

5. Sponges are divided into Calcispongiæ and Silicispongiæ according to the character of the skeleton.

PHYLUM III. CŒLENTERATA (CNIDARIA, NEMATOPHORA).

The animals belonging to the cœlenterates were formerly called Zoophyta (plant-animals). They were united by Cuvier with the Echinoderma to form the type Radiata, a union which Leuckart, the father of the name Cœlenterata, set aside because a special intestine and a special body cavity occur in the Echinoderma, while in the Cœlenterata there is but a single system of cavities in the body. Each of the three names indicates certain important characters of the group.

(1) The name Zoophyta was selected with regard to the general appearance. Most cœlenterates, like the plants, are fixed and form bush-like or mossy colonies by incomplete budding. This resemblance is but superficial, for in any accurate investigation there cannot be the slightest doubt of the animal nature of any Cœlenterate. The name therefore must not be understood to imply that these are doubtful forms which stand on the border between plants and animals. Besides, there are not only fixed but free-moving forms which swim in the water with great ease.

(2) Most Cœlenterata are radially symmetrical. There is a main body axis one end of which passes through the mouth and the other through the blind end of the digestive tract, and the organs of the body are radially arranged around this so that the body may be divided into symmetrical halves by numerous planes. In the higher Cœlenterata this may be replaced by a biradial symmetry or even by bilaterality (Ctenophora, many Anthozoa).

(3) The term Cœlenterata is given these animals because they contain a single continuous cœlenteron or gastrovascular cavity. In the simplest species this is a wide-mouthed sac into which food passes for digestion. The single opening into it serves at once as mouth and anus; the sac itself is the alimentary tract. Frequently lateral diverticula or branched canals are given off from the central sac which distribute the nourishment to the peripheral parts of the body, and thus functionally replace the vascular system of higher forms.

Since this gastrovascular system is primarily for nourishment, it is an error to call it a body cavity and to say that the cœlenterates are stomachless. On the other hand, the term 'cœlenteron,' that is a cavity which is at once gastric and cœlomic (p. 158), is perfectly defensible, since in many higher animals which possess a true body cavity this is seen in development to arise as diverticula from the primitive stomach (enteron). Since such diverticula occur in cœlenterates without becoming independent, one can say that the gastrovascular system consists not only of intestinal portions but, *in potentia,* of the cœlom as well.

To even a superficial observation the Cœlenterata are more clearly animals than are the sponges. The single animals, though often united in colonies, and fixed to some support, are capable of quick and energetic motion. These movements are most striking in the tentacles—long tactile threads, in the neighborhood of the mouth, which have the functions of feeling for food, grasping it, and conveying it to the mouth. The means of killing the prey are the cnidæ, nematocysts, or nettle cells (fig. 171), which with rare exceptions in Protozoa, Turbellaria, and molluscs occur in no other group. These structures, of great systematic importance, are oval vesicles with fluid contents and firm membrane. Each is drawn out at one end into a long tube, so delicate as to appear as a thread (hence an additional name, thread cells). This thread is sometimes armed throughout its length with retrorse hooks, or it may have only a few stronger hooks on its basal portion, which is thicker than the rest. In the resting stage the thread is spirally coiled inside the cell. On stimulation the thread is quickly extended ('explosion of cell') and produces a wound into which passes the irritating fluid contents. Some cœlenterates (*e.g. Physalia*) can produce in this way very painful nettling even in man.

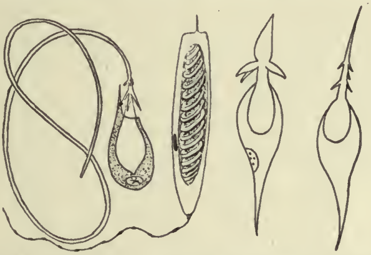


FIG. 171.—Nettle cells of Cœlenterata (After Hertwig, Lendenfeld, and Hamann.)

The nettle capsule arises as a plasma product inside a cell. When fully developed the nettle cell extends to the surface and ends with a tactile process (cnidocill) which upon contact stimulates the protoplasm and causes the explosion. The cell itself is frequently enclosed by a muscular sheath or a network of muscle fibres.

Among the cœlenterates both sexual and asexual reproduction may occur, the latter usually by budding, more rarely by division. Sexual and asexual types of reproduction can be combined in the same species, producing an alternation of generations.

In comparison with the sponges the Cœlenterata may be called epithelial organisms. A mesoderm ('mesoglœa') may be entirely lacking or may have but a subordinate development. The ectoderm and entoderm, on the other hand, are the important tissues—producing muscles, nerves, sense organs, sexual products and cnidæ. Hence the group is often called Diploblastica—two-layered animals.

Class I. Hydrozoa (Hydromedusæ).

According to varying standpoints the Hydrozoa can be placed either higher or lower than the Anthozoa in the system, since in the former group two forms are frequently introduced into the life history, one agreeing well in structure with the Anthozoa, the other standing on a higher grade. The first is the sessile and usually colonial polyp, the second the free-swimming medusa, well provided with sense organs. These are usually related to each other by an alternation of generations. The polyp is asexual and by budding produces medusæ; the medusa, on the other hand, is the sexual stage, and from its eggs polyps arise.

The polyp of the Hydrozoa is the hydropolyp, forming in the branch of cœlenterates an important archetype from which all other conditions—medusæ, scyphopolyp, and even the coral polyp—may be derived. Our best example of this is the fresh-water *Hydra,* so common in pools and streams. The body (fig. 172) is a sac, the hinder closed end of which, the pedal disc, is used for attachment. The other end bears the mouth which leads to the internal gastrovascular (digestive) cavity. Around the mouth is a circle of tentacles used in capturing food (mostly small crustacea). These are outgrowths of the body wall; the circle dividing the body into a peristome inside the circle and a column constituting the rest of the outer wall.

Hydra has but two body layers (fig. 173), an entoderm of flagellate cells lining the gastrovascular space, and the ectoderm covering the outer surface. Between the two is the supporting layer (mesoglœa), a structureless membrane without cells and hence not a body layer. Both layers consist of epithelial muscular cells (cf. p. 92), the basal ends of which are produced into smooth muscle fibres, those of the ectoderm running lengthwise, those of the entoderm around the body. The ectoderm further contains ganglion, nettle and sex cells. The nettle cells on the tentacles are crowded into small ridges or batteries. The sex cells (at certain times) produce swellings on the column; a circle of male swellings close beneath the tentacles, the female cells farther down the column (fig. 172). Individuals reproducing by budding are more common than the sexually mature (fig. 90). Small elevations appear on the column, enlarge, form tentacles, and at last a mouth, after which they may separate from the parent.

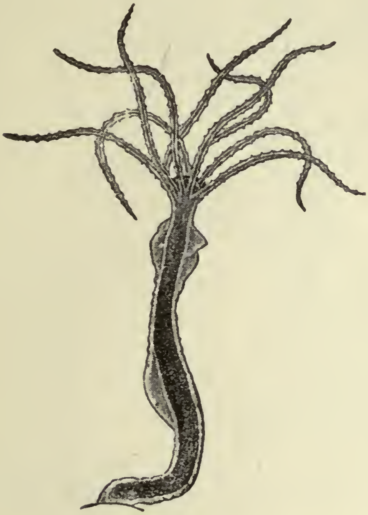


Fig. 172.

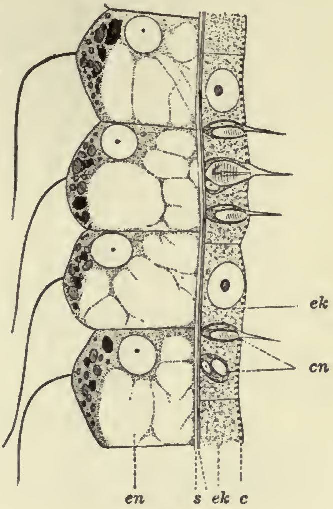


Fig. 173.

Fig. 172.—*Hydra viridis*,* testes above; ovarian enlargement below.
Fig. 173.—Body layers of *Hydra*. (After Schulze, from Hatschek.) *c*, cuticula; *cn*, nettle cells; *ek*, ectoderm; *en*, entoderm; *s*, supporting layer.

In the sea are numerous hydroid polyps which, while agreeing in the main with *Hydra*, are distinguished from it in two important respects: (1) they do not directly produce sexual organs; (2) they reproduce asexually, and by incomplete budding form persistent colonies. In this formation of colonies a series of parts have arisen which require special designations (fig. 174). The separate animals are the *hydranths*, and are connected together by a system of tubes, the *cœnosarc*, which, like the hydranths, consist of ectoderm, entoderm, and mesoglœa, and since the gastrovascular space continues in them, these effect a distribution of food throughout the colony. The cœnosarcal tubes may creep over some support (stone, alga, snail-shell, etc.) and form a network, the *hydrorhiza*, or it may stand erect and tree-like, forming a *hydrocaulus*. Usually both hydrorhiza and hydrocaulus occur in the same colony.

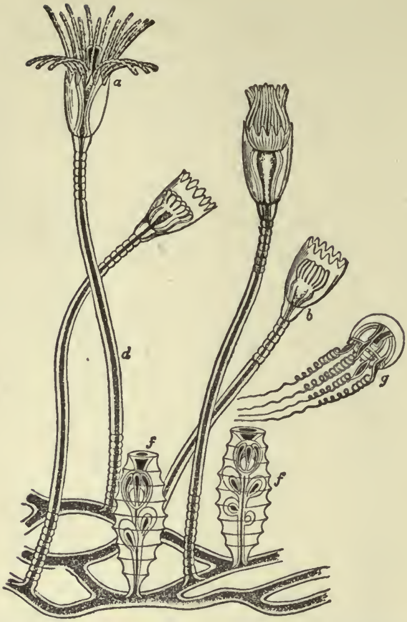


FIG. 174.—*Campanularia johnstoni.* (After Allman.) *a*, hydranth with hydrotheca; *b*, retracted; *d*, hydrocaulus; *f*, gonotheca, with blastostyle and medusa buds; *g*, free medusa.

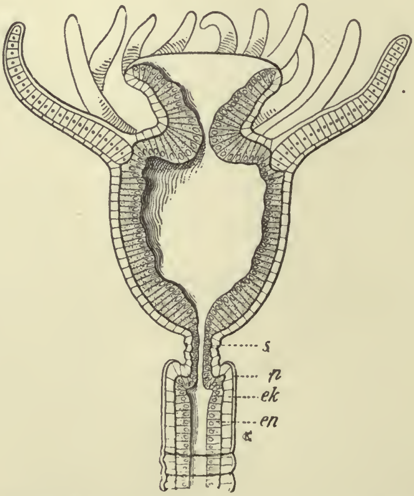


FIG. 175.—Section of *Eudendrium ramosum.* *ek*, ectoderm; *en*, entoderm; *p*, perisarc; *s*, supporting layer.

Usually the colony is strengthened and protected by the perisarc, a cuticular tubular secretion of the ectoderm. In some (fig. 175) the perisarc stops at the base of the hydranth; in others (fig. 176) it expands distally into a wide-mouthed bell, the hydrotheca, into which the hydranth may retract at times of danger. In rare cases this perisarc may be greatly increased and calcified, forming large coral-like masses with openings from which the hydranths may protrude (fig. 177).

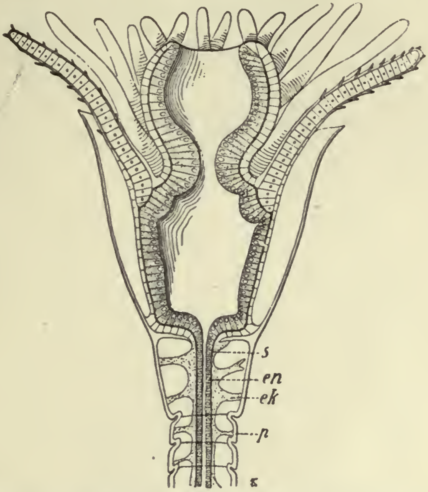


FIG. 176.—*Campanularia geniculata*. *ek*, ectoderm; *en*, entoderm; *p*, perisarc, expanded around hydranth to a hydrotheca; *s*, supporting layer.

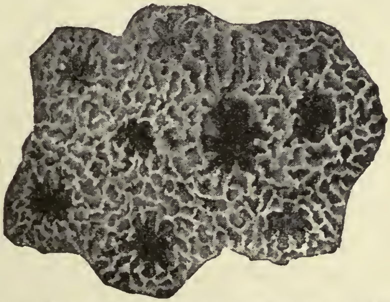


FIG. 177.—A bit of *Millepora alcicornis*, enlarged. (After Agassiz.)

The lack of sexual organs, which distinguishes the marine species from the fresh-water *Hydra*, is explained by the fact that sexual individuals of special form are produced from the colony by budding. These, the medusæ, may separate early from the colony and swim freely. A medusa (figs. 178, 179) has the form

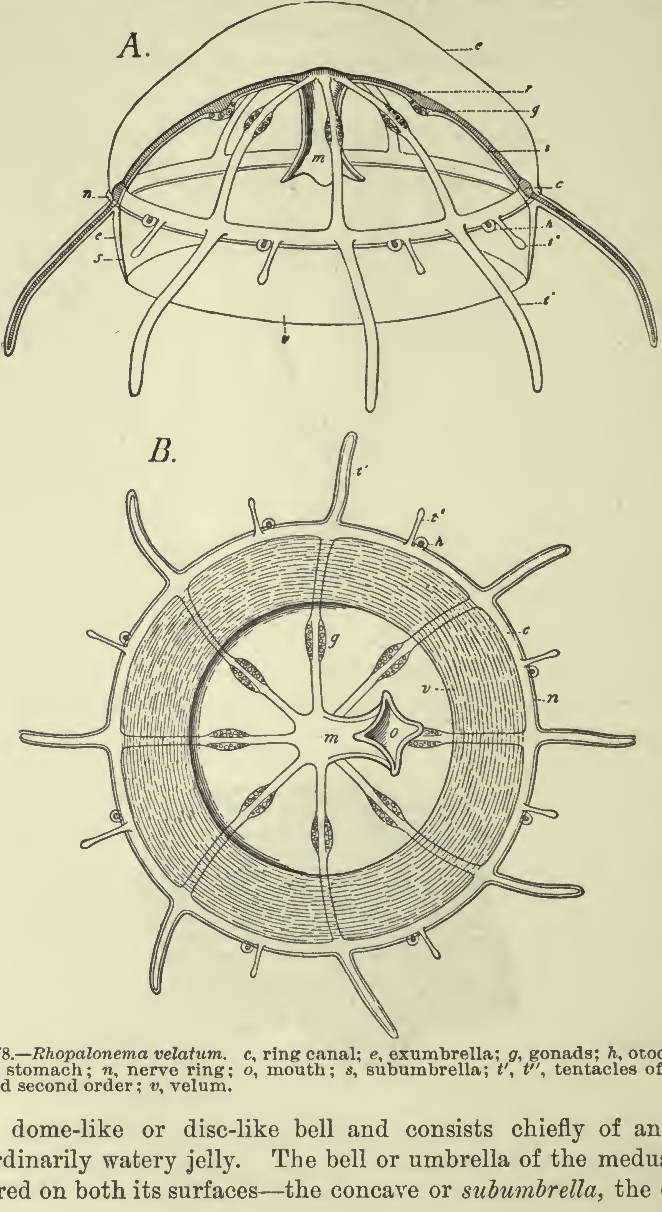


FIG. 178.—*Rhopalonema velatum.* *c*, ring canal; *e*, exumbrella; *g*, gonads; *h*, otocysts; *m*, stomach; *n*, nerve ring; *o*, mouth; *s*, subumbrella; *t'*, *t''*, tentacles of first and second order; *v*, velum.

of a dome-like or disc-like bell and consists chiefly of an extraordinarily watery jelly. The bell or umbrella of the medusa is covered on both its surfaces—the concave or *subumbrella,* the convex or *exumbrella*—with ectodermal epithelium. At the margin of the bell the sub- and exumbrellar ectoderm is produced into a two-layered sheet with a central opening, the *velum* or *craspedon* (fig. 178, *B*, *v*) of systematic importance, since these medusæ are often spoken of as Craspedota. Tentacles (usually 4, 8, or multiples in number) also arise from the edge of the bell just outside the velum.

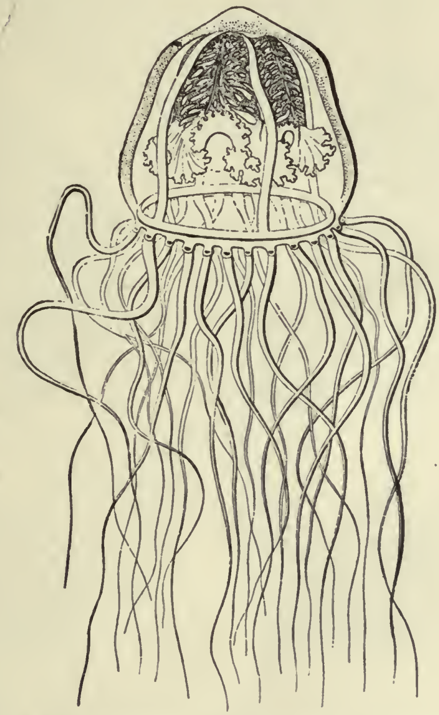


FIG. 179.—*Tiara pileata.* (After Haeckel, from Hatschek.)

Comparable to the tongue of the bell or the handle of the umbrella is the *manubrium,* hanging from the highest point of the subumbrella and bearing the mouth at its tip. It contains the chief digestive space from which radial canals run on the subumbrellar surface to a ring canal in the margin of the umbrella. The radial canals are usually four in number, but in some species the number is increased during growth even to a hundred or more. Manubrium and canals are lined by entoderm, which also extends into the tentacles and forms their axes.

All other important organs arise from the ectoderm. Gonads arise in many species (fig. 179) from the ectoderm of the manubrium; in others from the same layer covering the subumbrellar surface of the radial canals (fig. 178), forming in either case conspicuous, often orange or red, thickenings. Longitudinal ectodermal muscles move the tentacles in a snaky fashion, whence the name medusa. Circular striped muscles run on the subumbrellar side of bell and velum, causing the characteristic motion. By this contraction the bell becomes more arched and narrowed, while the velum (which hangs down when at rest—fig. 178, *A*) contracts like a diaphragm across the mouth of the bell (fig. 178, *B*). Since water is thus forced out through the opening the medusa is forced forward by the reaction.

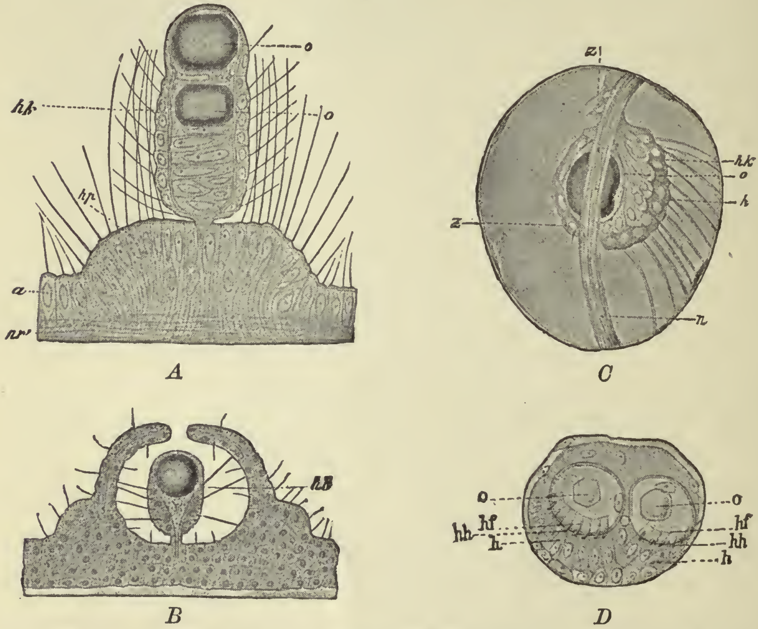


FIG. 180.—Otocysts of Medusæ.—*A*, *Cunina*; *B*, *Rhopalonema*; *C*, *Carmarina* (Trachymedusæ); *D*. *Octorchis* (Leptomedusan). *a*, epithelium; *h*, auditory cells; *hf*, origin of hairs; *hh*, auditory hairs; *hp*, auditory cushion; *o*, otoliths; *n*, auditory nerve; *nr*, nerve ring.

The circular muscles of umbrella and velum are separated by the nerve ring, with which are connected the sensory organs—eyes of the simplest type; red pigment spots with or without a lens (fig. 81); and open or closed auditory vesicles (otocysts). Tactile hairs are abundant on the tentacles.

The auditory organs are of two types, both beginning as free organs and receiving their highest development as closed vesicles (otocysts). One type, the tentacular organs, occur in the Trachymedusæ, the other, or velar organ, in the Leptomedusæ. The tentacular organs are modified tentacles, the entodermal axis of which forms the otoliths and the ectodermal covering the sense cells. In the Æginidæ (Fig. 180, *A*) the club-like tentacles, seated on an auditory cushion, project freely into the water; in the Trachynemidæ (Fig. 180, *B*) they are partially transformed into vesicles by the upgrowth of epithelium, and in the Geryonidæ (Fig. 180, *C*) they are completely enclosed and are sunk in the jelly of the bell. The velar organs of the Leptomedusæ are placed on the subumbrellar surface of the velum. They may be either simple pits (Fig. 180, *B*), or the mouths of the pits may close (Fig. 180, *D*). In these both sense cells and otoliths are ectodermal. Eyes and otocysts occur in different forms, a fact which formerly lead to a division of medusæ into ocellate and vesiculate groups.

While polyps and medusæ apparently differ so greatly from each other, their morphology shows that the medusæ are only highly modified polyps adapted to a swimming life. The long axis of the polyp has been greatly shortened (fig. 181) and the cylindrical body developed into a disc; the mesoglœa of column and disc thickened to a conspicuous layer of jelly; while manubrial cavity, radial and ring canals are to be interpreted as remnants of the large gastrovascular space of the polyp, obliterated in part by the pressure of the mesoglœa. To the parts thus formed only the velum and sense organs are added.

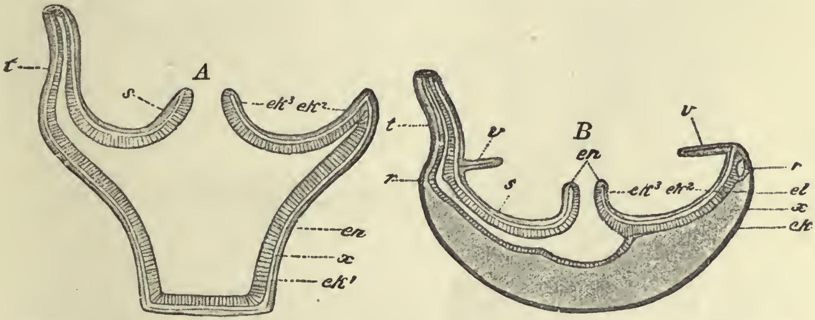


FIG. 181.—Diagram of sections of (*A*) a polyp and (*B*) a medusa. *ek*, ectoderm; *ek′*, of exumbrella; ek^2, of subumbrella; ek^3, of manubrium; *el*, endoderm (cathamnal) layer arising from obliteration of digestive space; *en*, entoderm; *r*, ring canal; *s*, subumbrella; *t*, tentacles; *v*, velum; *x*, supporting layer (gelatinous in *B*).

This comparison of medusa with polyp is of importance in understanding the development, which usually is complicated by an alternation of generations. From the eggs of the medusæ a small ciliated embryo (planula) escapes, which becomes attached, develops mouth and tentacles, and, by budding, produces a hydroid colony. This hydroid colony lacks sexual organs. It produces by budding the sexual individuals, the medusæ, which separate and swim freely. Since polyp and medusæ are morphologically comparable, there is a time before the escape of the medusæ when the colony is polymorphic, consisting of asexual individuals (hydranths) which reproduce only asexually and of others which have taken over the sexual reproduction (medusæ). Hence we conclude that the alternation of generations here has arisen from a division of labor or polymorphism of individuals originally of equivalent value, in which some individuals (the sexual) have separated and acquired a peculiar structure.

While alternation of generation has arisen from polymorphism, it can again produce it. This occurs when the medusæ, instead of separating, remain permanently attached to the colony. They then degenerate into 'sporosacs,' which always lack mouth, tentacles, and velum (fig. 182), often also radial and ring canals, so that at last there remains only the manubrium ('spadix') and the sexual organs, the latter enveloped by the rudiments of the umbrella. Since medusæ and sporosac replace each other in closely allied species, a common name, *gonophore,* has been applied to both.

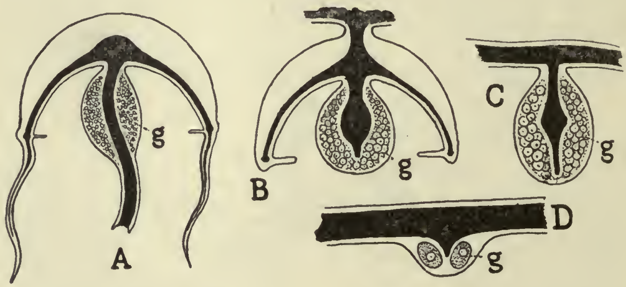


Fig. 182.—Comparison of a medusa and a sporosac (orig.). *A*, fully developed medusa; *B*, medusa with the manubrium closed, still attached to the blastostyle; *C*, medusa reduced to a simple manubrium (sporosac); *D*, last stage, eggs being produced in the body wall (*Hydra*).

This developmental history may be modified in two ways: either the polypoid or the medusan generation may be suppressed. In the first case we have polyps which reproduce both sexually and asexually, in the other medusæ whose eggs develop directly into other medusæ. (A few medusæ may produce new medusæ by budding.) Thus we can have four conditions: (1) Polyps which produce sometimes asexually, sometimes sexually, but always polpys; (2) Medusæ which always produce medusæ; (3) Polyps and medusæ in alternating generations; (4) Polyps and sessile medusæ (sporosacs) united in a polymorphic colony.

The Hydrozoa are almost exclusively marine. The colonial forms occur mostly on rocky coasts down to a depth of 100 fathoms, but have been found in water 4000 fathoms deep. The medusæ belong to the pelagic fauna. For a long time the only fresh-water species known belonged to the cosmopolitan genus *Hydra*, but more recently both hydroid (*Protohydra ryderi*,* America; *Polypodium hydriforme*, Russia) and medusan forms (*Limnocodium sowerbyi*, Brazil; *Limnocnida tanganyicæ*, Africa; *Halomises lacustris*, Trinidad) have been found. *Cordylophora lucustris** occurs in the brackish waters of Europe and America.

The Hydrozoa may be classified according to characters, derived either from the hydroid or the medusan stage. The former basis gives us four groups:

(1) Hydraria. Polyps with asexual and sexual reproduction; no persistent colonies, no perisarc, no gonophores (fig. 172).

(2) Tubulariæ. Mostly colonial, with perisarc but without hydrothecæ. Reproduction by gonophores (medusæ or sporosacs, figs. 91, 175).

(3) Campanulariæ. Colonial, with perisarc and hydrotheca. Reproduction by gonophores arising in special perisarcal envelopes, the gonotheca (figs. 174, 176).

(4) Hydrocorallina. Colonial, with massive, calcified perisarc, resembling coral. Reproduction by sporosacs or short-lived medusæ.

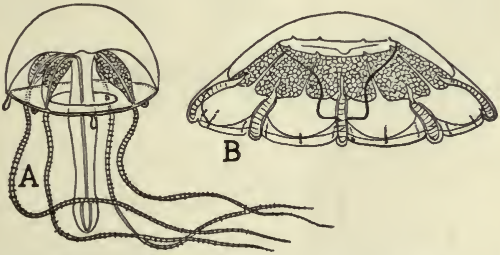


FIG. 183.—American Trachy and Narcomedusæ. *A*, *Liriope scutigera*. (After Fewkes.) *B*, *Cunocantha octonaria*. (After Brooks.)

The characters derived from the medusæ also give five groups:

(1) Anthomedusæ (Ocellatæ). Gonads on the manubrium; no auditory organs; eyes usually present; polyp generation present.

(2) Leptomedusæ. Gonads on radial canals; usually velar auditory organs; polyp generation present.

(3) Trachymedusæ. Gonads on the radial canals; tentacular auditory organs; develop directly to medusæ (fig. 183, *A*.)

(4) Narcomedusæ. Gonads on the manubrium or gastral pouches; tentacular auditory organs; no polypoid stage (fig. 183, *B*.)

(5) Siphonophora. Polymorphic, free-swimming colonies of Anthomedusæ; no polyp generation.

From this it is seen that there are medusæ without polyp stages and polyps without medusæ, so that a true system must take into account both these features. When this is done and life histories are traced it is seen that the Anthomedusæ and the Tubulariæ are connected by an alternation of generations, and the same holds good for Leptomedusæ and Campanulariæ. There are three groups—Trachymedusæ, Narcomedusæ, and Siphonophora—without a hydroid stage, and two in which the polyp plays the chief rôle, the medusa being rudimentary in the Hydrocorallinæ, lacking in the Hydraria. The hydroid polyps are usually but a few millimetres or fractions of a millimetre in size, but the huge *Monocaulis imperator*, of the deep seas, a yard in length, forms an exception. The colonies are usually only a few inches in extent. The medusæ have bells varying between a millimetre and a few inches in diameter, reaching in *Æquoria forskalea* a diameter of sixteen inches.

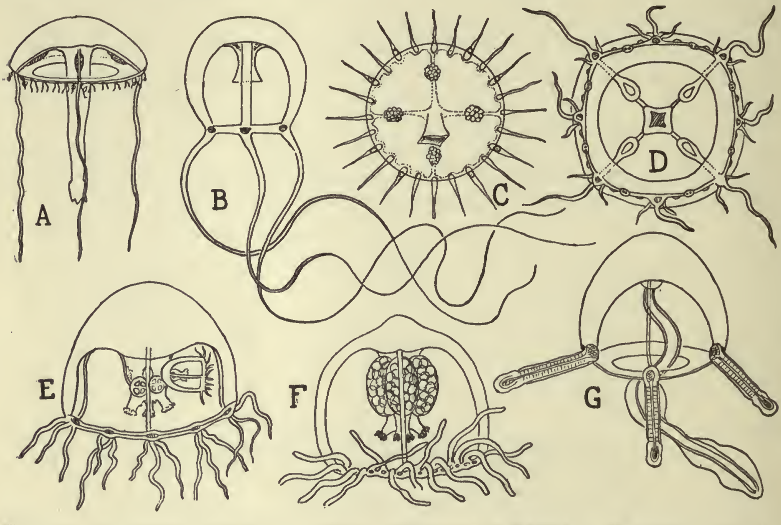


FIG. 184.—American hydrozoan medusæ. (Mostly after Fewkes.) *A, Eutima gracilis; B, Hydrichthys mirabilis; C, Obelia; D, Euchilota ventricularis; E, Lizzia grata; F, Turritopsis nutricola; G, Dipurena strangulata.*

Order I. Hydraria.

Until recently only the cosmopolitan species of *Hydra* were known. During most of the year they reproduce by budding (fig. 90), only occasionally developing gonads (fig. 172). The eggs remain in connexion with the mother during segmentation, and later form an embryonal shell, protecting them from drought or cold. In this 'encysted stage' they can be distributed by wind or water birds. These animals formed the basis of the celebrated researches of Trembley on regeneration. He showed that small portions when they contained both body layers could regenerate the whole animal. His experiments upon turning the animals inside out have not been fully confirmed; for in such cases the layers resume their normal positions. *Hydra grisea* * (*fusca*), large brown species; *H. viridis*,* green, from the presence of symbiotic algæ. *Protohydra ryderi*,* without tentacles. *Polypodium hydriforme*, parasitic on sturgeon eggs in Russia, needs more study. The marine *Haleremita cumulans* may belong here.

Order II. Hydrocorallinæ.

Exclusively marine, forming colonies of thousands of individuals whose calcareous skeletons so closely resemble true corals that they were associated with them until the animals were studied. *Millepora alcicornis*,* stag-horn coral, in Florida. The rosy *Stylasters* occur in tropical seas.

Order III. Tubulariæ = Anthomedusæ (Gymnoblastea).

As a rule these colonial forms with perisarc but without hydrotheca produce anthozoan medusæ, but there are forms like *Clava* * (pink, on rockweed) and *Hydractinia* * (on shells inhabited by hermit crabs) which have sporosacs. Indeed the genera *Corymorpha* * and *Monocaulis* * are only differentiated by the existence of medusæ in the former and of sporosacs in the latter. In the forms with alternation of generations different names are applied to the hydroid and medusan stages as follows:

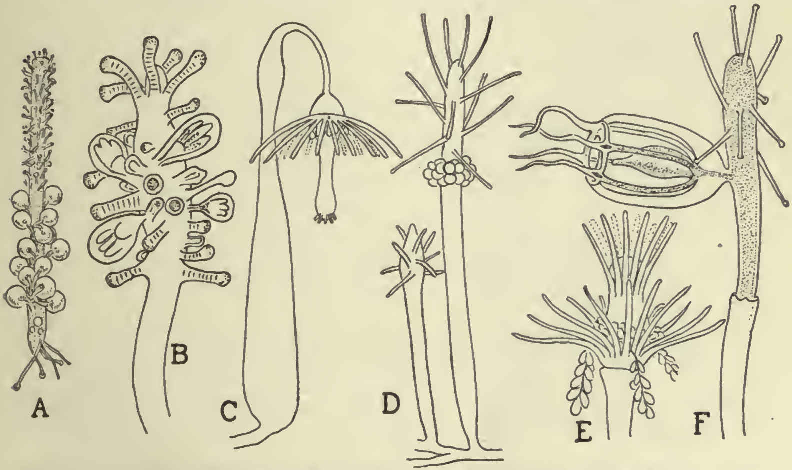


FIG. 185.—American Tubularian hydroids. *A, Myriothelia phrygiana* (after Danielssen and Koren); *B. Sarsia rosaria* (after Fewkes); *C, Monocaulis pendula* (after Agassiz); *D, Clava leptostyla; E, Parypha crocea; F, Podocoryne mirabilis* (after Agassiz).

HYDROID.	MEDUSA.
Pennaria.	*Globiceps.*
Syncoryne.	*Sarsia.*
Bougainvillea.	*Hippocrene, Margelis.*
Gemmelaria.	*Gemmaria.*
Podocoryne.	*Dysmorphosa.*

Other common genera in American waters are, of hydroids, besides those mentioned, *Eudendrium*, *Tubularia*, and *Thamnocnida;* of medusæ, *Tiaris*, *Turritopsis*, *Dipurena*, *Lizzia*, *Nemopsis*, and *Hydrichthis.*

Order IV. Campanulariæ = Leptomedusæ (Calyphoblastea).

These forms are readily distinguished from the last by the fact that they are always colonial and possess hydrothecæ, the medusæ always being Leptomedusæ (p. 239). A peculiarity of the group is the existence of gonothecæ, closed perisarcal envelopes, inside which the gonophores arise from the blastostyle, a specialized polyp, without mouth or tentacles (fig. 174, *f*). The typical Campanulariæ produce medusæ, while some forms, like *Thaumantia* * and *Æquoria* * have no hydroid stage, and on the other hand *Sertularia* * and *Plumularia* * have no medusa stage.

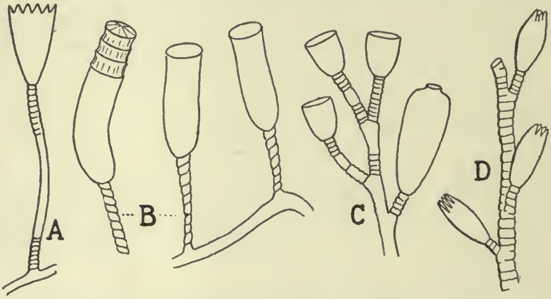


FIG. 186.—American Campanularians. (After Verrill.) *A. Clytia noliformis ; B, Calycella syringa; C, Obelia dichotoma ; D, Opercularella pumila.*

Other common genera, *Clytia*,* *Diphasia*,* and *Aglaophenia* * among hydroids ; *Obelia*,* *Tima*,* *Rhegmatodes* * among medusæ. Possibly the fossil group of GRAPTOLITES belongs near here. Only the perisarc is known, and this is composed of hydrothecæ, in which it is supposed the hydranths occurred.

Order V. Trachymedusæ.

These medusæ, mostly from warmer seas, have no hydroid stage. The characters are given on p. 239, *Trachynema*, *Liriope* * (fig. 183), and *Campanella* in our own waters, *Geryonia*, etc., in Europe.

Order VI. Narcomedusæ.

In addition to the characters on p. 239 may be added the fact that the tentacles arise from the outside above the rim of the bell. *Cunocantha* * (fig. 183), and *Cunina* * in our warmer waters, *Ægina* in Europe.

Order VII. Siphonophora.

The Siphonophora are among the most beautiful of pelagic animals, some transparent, some brightly colored. Each (fig. 187) consists of a colony of individuals springing from a common cœnosarcal tube which is strongly muscular and contains a central canal lined with entoderm by which the members of the colony receive their nourishment. At one end the tube is usually closed by a float filled with air, the *pneumataphore*, which acts as a hydrostatic apparatus, and keeps the colony vertical in the water.

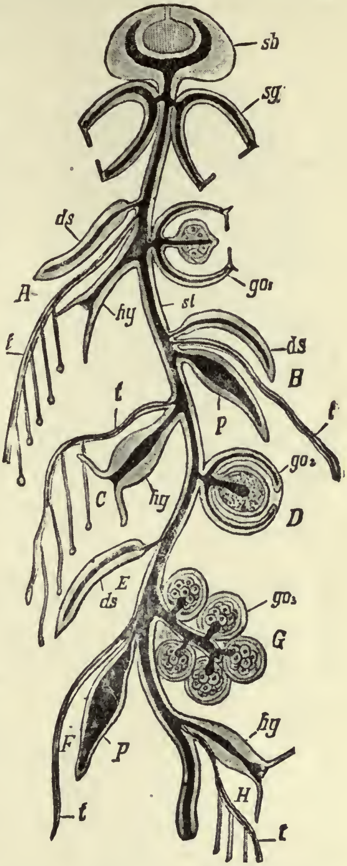


Fig. 187.—Diagram of Siphonophore. (From Lang.) *A–H*, groups of different individuals; *ds*, covering scales; *gc*, gonophores; *hy*, feeding polyps; *p*, 'tasters' (digestive); *sb*, float; *sg*, swimming bell (nectocalyx); *st*, stalk.

The individuals, springing from the cœnosarcal axis, perform different functions and hence have different structures. Close behind the float commonly come several swimming bells (*nectocalyces*) which retain of medusal structures only those (bell, velum) necessary for swimming and those (ring and radial canals) for the distribution of nourishment received from the common tube. Then come, scattered through the colony, the covering scales, for protection, firm gelatinous plates which have lost the ring canal, the muscles, and the bell shape of the medusæ. Food is taken by wide-mouthed feeding tubes (*hy*) which may be compared to polyps (fig. 57) or the manubrium of a medusa. They digest the food by means of large masses of glands ('liver bands') and convey it by the central tube to all the members of the colony. At the base are long muscular tentacles (*t*) from which small lateral threads depend, each ending in a brightly colored swelling, the nettle head, composed of large, closely packed nettle cells. These are the cause of the nettling produced by the siphonophores, which in many is so severe as to be feared by man. The 'feelers' (*p*) recall mouthless polyps and manubria; they are very sensitive and mobile and, while tactile, apparently in some cases are digestive organs. Latest to develop in the colony are the sexual bells. They are usually brightly colored and resemble small mouthless

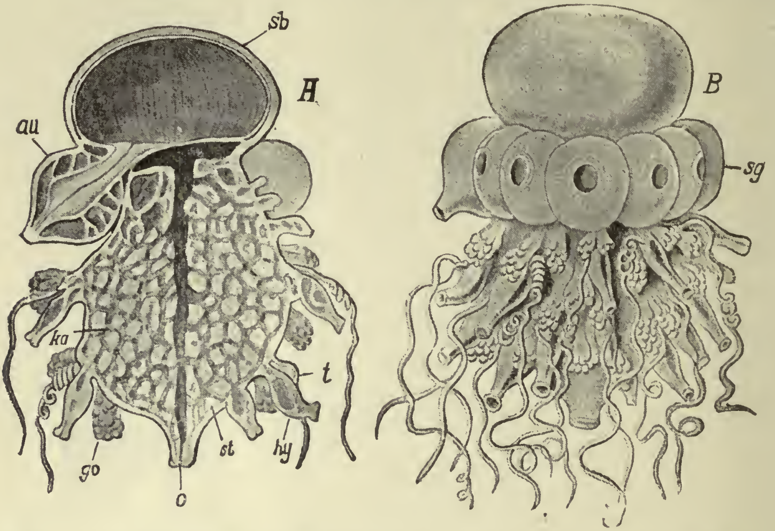


Fig. 188.—*Stephalia coronata*. (After Haeckel, from Lang.) *A*, in section; *au*, canal to float; *ka*, canal system of stalk; *o*, mouth; other letters as in fig. 188.

Anthomedusæ without tentacles. They but rarely (*Chrysomitra*) separate from the colony, but usually persist as more or less reduced sporosacs.

From this it follows that the Siphonophora afford fine examples of division of labor and of the consequent polymorphism of individuals. This can indeed be carried so far that many convey the impression of being individuals with a multiplicity of organs. The Siphonophora are all marine, and occur most abundantly in tropical seas.

Sub Order I. PHYSOPHORÆ (Physonectæ). Float present, but small; next a large series of swimming bells, and then the other members of the colony. *Physophora*, *Agalmia*, *Nanomia* * (fig. 189).

Sub Order II. CALYCOPHORÆ (Calyconectæ). Float lacking; one or two large swimming bells; the other individuals in groups which frequently separate before becoming mature, and were once regarded, under the name *Eudoxia*, as distinct animals. *Praya*, *Diphyes* * (fig. 189), in warmer seas.

Sub Order III. CYSTONECTÆ. Float greatly enlarged; the cœnosarcal tube reduced, the individuals (no covering scales nor swimming bells) being attached to the under side of the float. *Physalia*, the Portuguese man-of-war, occurs as far north as New England. It is brightly colored, and, sitting high on the water, is driven about by the wind. It stings very severely.

Sub Order IV. DISCONANTHÆ. Float a flattened disc with concentric air chambers; the manubrium projects from the centre of the lower surface of the float. *Porpita*,* with circular disc. *Velella** (fig. 189), the paper sailor, has a triangular 'sail' on the disc. Both are tropical and subtropical.

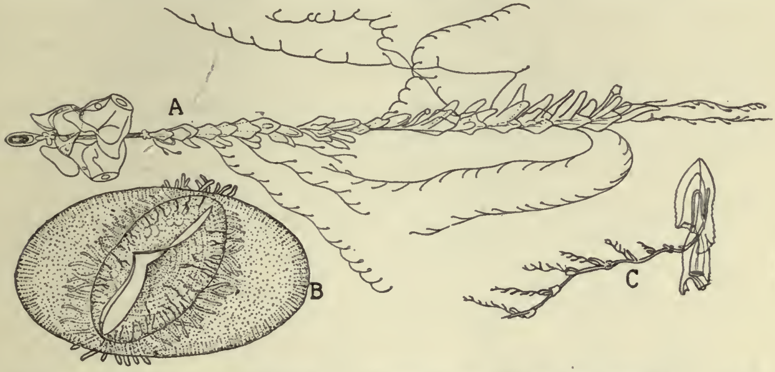


FIG. 189.—American siphonophores. *A, Nanomia cara.* (After A. Agassiz.) *B. Velella meridionalis.* (After Fewkes.) *C, Diphyes praya.* (After Fewkes.)

Class II. Scyphozoa (Scyphomedusæ).

The Scyphozoa parallel the Hydrozoa in that they frequently have an alternation of generations. The asexual generation is the scyphopolyp or scyphostoma, the sexual an acraspedote medusa. In contrast to the Hydrozoa the asexual stage plays a subordinate

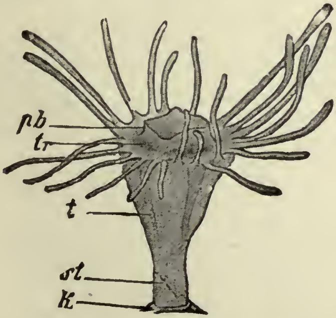


FIG. 190.

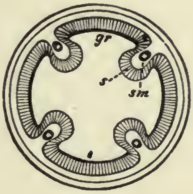


FIG. 191.

FIG. 190.—Scyphostoma of *Aurelia aurita.* (From Korschelt-Heider.) *k*, perisarc cup; *pb*, proboscis; *s*, stalk; *t*, gastral folds; *tr*, ectodermal funnels.

FIG. 191.—Section of Scyphostoma. (From Hatschek.) *gr*, gastric pouches; *s*, gastric folds; *sm*, muscles.

rôle; it is closely similar, even in the most different species, and can even be lost (*Pelagia*), while the medusæ are always well developed and present great variety of form.

The scyphostoma (figs. 190, 191) recalls superficially *Hydra*, but is distinguished externally by a small perisarcal cup in which the aboral end is placed. Internally there are four longitudinal folds projecting into the gastral cavity and extending from the margin of the mouth to the opposite pole. These septa or *tæniolæ* appear in cross-section as small folds of entoderm supported by a process of the supporting layer. They are important morphologically, since in budding they produce the gastral tentacles (*phacellæ*) of the medusæ. Further, they are the first appearance of the septal system, so strongly developed in the Anthozoa.

The acraspedote medusæ are large forms (four inches to four feet or more in diameter) with an arched umbrella often of almost cartilaginous consistency. They are distinguished from the craspedotes externally by notches in the margin of the umbrella, dividing the periphery into lobes. In the common forms at least eight lobes occur (figs. 192, 193), each notched at its tip, and in the notch the sensory pedicels bearing both ears and eyes and covered by a lappet. In some (fig. 193, *I, II*) the sensory lobes follow each other, but in others the intermediate region is also notched, the sensory pedicels then being found only on careful search (fig. 194). Tentacles, when present, spring from the notches of the intermediate region.

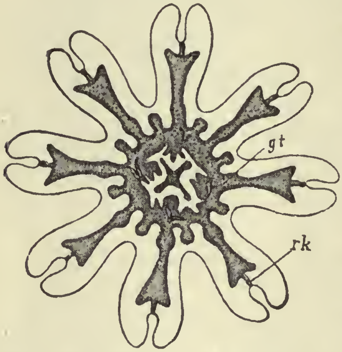


FIG. 192.—Ephyra of *Cotylorhiza*. (After Claus.) *gt*, gastral tentacles (phacellæ); *rk*, marginal (sensory) body.

The sensory pedicels predicate the position of eight principal radii, of which four are called the perradii, the four alternating with them the interradii. Adradii are radii lying between the principal radii.

The lobing of the umbrella influences all other structures. There is no velum (hence these are called Acraspedia), its place being taken by a thick muscular mass (fig. 86, *m*) on the subumbrellar surface. Instead of a nerve ring there are eight nerve centres connected with the sensory pedicels. Each of these pedicels (fig. 195) is a modified tentacle with an entodermal

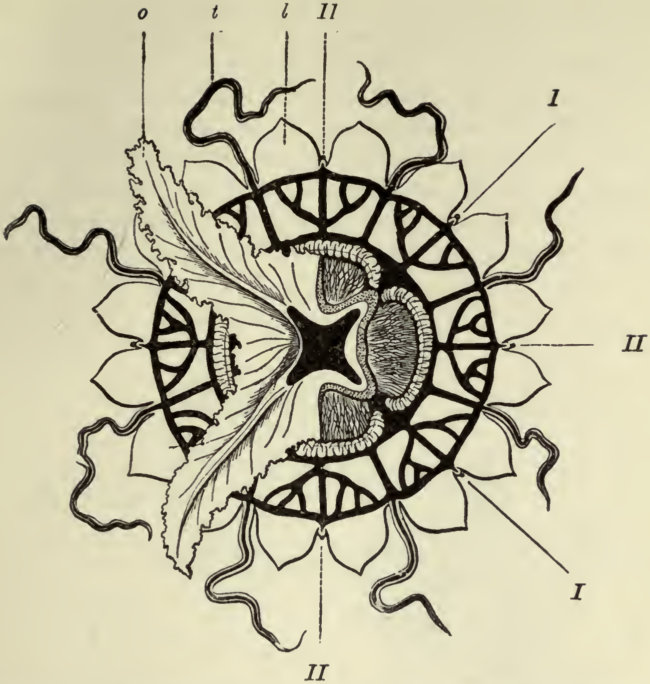


FIG. 193.—*Ulmaris prototypus.* (From Hatschek.) *I*, radii of first order (perradii); *II*, radii of second order (interradii); *l*, marginal lobes; *o* oral lobes (cut away on right side); *t*, tentacles (adradial); the gonads (right side) are interradial.

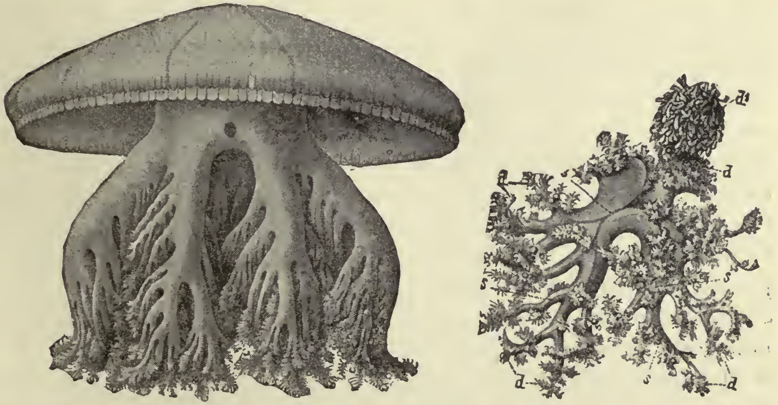


FIG. 194.—*Polyclonia frondosa* * and one of its branching oral lobes, showing the closed grooves (*s*). (After Agassiz)

axis and an outer layer of ectoderm. The entoderm forms an otolith sac at the tip, while the ectoderm furnishes a nervous cushion of ganglion cells and fibres and usually a simple eye spot. Less evident is the effect of the lobing on the internal organs. The gastrovascular system begins with a quadrate or X-shaped mouth (fig. 193). The perradial angles of the mouth are usually produced into long curtain-like oral tentacles of great use in the capture of food. The 'stomach,' which begins just inside the mouth, gives off four interradial (i.e., alternating with the corners of the mouth) pouches, the gastrogenital pockets. The epithelium of these pouches produces on the one hand a group of small gastral tentacles (phacellæ), each extremely mobile and supported by an axis of mesoglœa; on the other plaited folds of the gonads, these being, in contrast to the Hydrozoa, of entodermal origin. In this the Scyphomedusæ show relationships to the Anthozoa. From the central digestive sac arise the peripheral portions. These consist in the larval medusæ (Ephyra stage, fig. 192) of eight radial canals to the sensory pedicels, and in most adult medusæ of these same pouches and eight others, adradial in position, to the tentacles. In some this primitive arrangement is complicated by an extensive network of tubes (fig. 193).

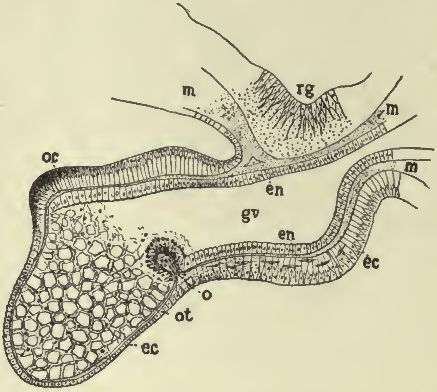


FIG. 195.—Sense organs of *Aurelia aurita*. (After Schewiakoff.) *ec*, ectoderm; *en*, entoderm; *gv*, gastrovascular space; *m*, supporting layer; *o*, cup eye; *oc*, pigment eye; *ot*, otolith sac; *rg*, olfactory groove.

In the species with an alternation of generations the egg produces a ciliated larva (fig. 196) which attaches itself and develops into a scyphostoma. This scyphostoma is always capable of terminal, and often of lateral, budding. The lateral buds always produce new scyphostomæ, the terminal, medusæ. In the latter the scyphostoma develops into a strobila, becoming divided by circular constrictions into a series of saucer-like discs, the young jelly-fish. As the successive discs become ready they separate from the pile and swim away as 'ephyræ.' At first the ephyræ (fig. 192) have only four gastral tentacles, parts of the gastral folds of the scyphostoma (p. 246); they lack marginal tentacles, but have the eight lobes and the corresponding sense pedicels. Since the ephyræ differ markedly from the adult medusæ and only gradually change into the sexual form, the alternation of generations is complicated by a metamorphosis. This metamorphosis persists in some cases (*Pelagia noctiluca*) where the alternation of generations is suppressed; the egg develops directly into an ephyra, which becomes transformed into the adult jelly-fish. On the other hand no case is known where the medusa generation is dropped out and the scyphostoma give rise sexually to other scyphostomæ.

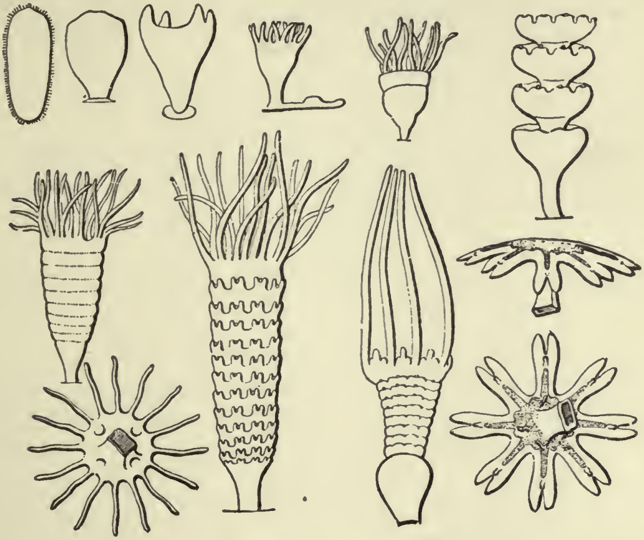


FIG. 196.—Development of *Aurelia aurita*. (From Hatschek.) First row, growth of planula to scyphostoma; below, strobilation (separation of ephyræ): left, oral view of scyphostoma; right, two ephyræ.

Some forms differ from the foregoing description in structure and apparently in development. Some have only four sensory bodies, the places of the other four being taken by tentacles. In these cases the sensory organs lie (Peromedusæ) in the same radii (*i.e.*, interradii) as the sexual organs or (Cubomedusæ) the sense organs are perradial. Lastly, some have no sensory organs, their place being either taken by tentacles or left vacant (Stauromedusæ). This shows that tentacles can replace sensory pedicels, and since they have essentially the same structure, they, like the cordylii of the Trachymedusæ, are modified tentacles.

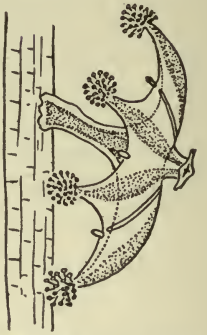


FIG. 197. — *Halyclystus auricularia.** (After Clark.)

Order I. Stauromedusæ (Calycozoa).

The best known forms are the Lucernariæ (fig. 197), whose exumbrellar surface is drawn out into a stalk by which the animals are attached. The disc is drawn out into eight lobes, each with a cluster of knobbed tentacles. Several species, dark green in color, occur in New England waters. The *Tesseridæ* (unknown in America) are free-swimming.

Order II. Peromedusæ.

Cup-shaped medusæ with four interradial sense bodies. Mostly high sea forms. *Pericolpa*, *Periphylla* in the Gulf Stream.

Order III. Cubomedusæ.

Sense organs perradial in position. Occurring in tropical and semitropical seas. *Charybdea* (fig. 198). Development unknown.

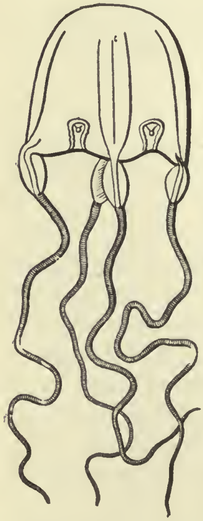


FIG. 198. — *Charybdea marsupialis.** (From Hatschek.)

Order IV. Discomedusæ.

These are the most abundant and richest in species of Scyphomedusæ and hence have served as the basis of the foregoing account. The order is subdivided according to the characters of the mouth. (1) CANNOSTOMÆ, mouth triangular without oral tentacles; shape and other features of the ephyra retained in the adult. *Nausithoë albida* (fig. 86) of Europe is noticeable because its scyphopolyp, described as *Stephanocyphus mirabilis*, is parasitic in sponges. *Linerges* and *Atolla* in the Gulf Stream. (2) SEMÆOSTOMÆ, mouth X-shaped with long fringed and folded arms at the corners. *Aurelia flavidula* * and *Cyanea arctica** common in New England, the latter, the 'blue jelly,' often very large; disc 7 feet in diameter, tentacles extending a hundred feet or more. *Pelagia* * in our warmer waters. (3) RHIZOSTOMEÆ, four oral arms, these branched dichotomously. The mouth and grooves on the arms closed by union of their edges so that many small sucking stomata remain through which nourishment is taken. *Stomolophus** and *Polyclonia frondosa** (fig. 194) on coral banks in our warmer seas.

Class III. Anthozoa (Actinozoa).

The Actinozoa, including the sea anemones, sea pens, and corals, are exclusively marine. With few exceptions they are sessile and form colonies, often of enormous size. In this as in appearance (fig. 199) they resemble the hydroid polyps. They have a pedal disc, column, tentacles, and peristome with central mouth. They are distinguished by their greater completeness in histological and organological differentiation. The Anthozoan polyp has a well-developed mesoglœa, the supporting layer of the hydroid being here a layer of connective tissue with numerous cells, giving the animals a tough fleshy consistency. Still more important as points of distinction are the presence of an œsophagus and septæ bearing mesenterial filaments and gonads.

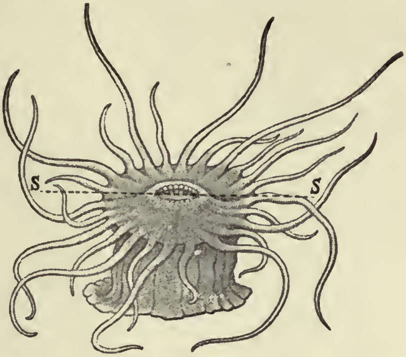


FIG. 199.—*Antheomorpha elegans.* *s*, *s*, sagittal plane.

The mouth lies in the centre of the peristome, and in shape is usually oval or slit-like. Hence there is a biradial symmetry—of importance in the architectonic of the polyp—for there is a sagittal axis (fig. 199, *s*, *s*) passing in the long axis of the mouth and a transverse axis at right angles to it. From the mouth the œsophagus hangs down into the body as a flattened tube and opens at its lower end into the wide gastrovascular cavity. In its development this œsophagus is an inflected part of the peristome and hence lined with ectoderm, and its lower end alone can be compared with the mouth of the hydrozoan (fig. 200).

The œsophagus is held in position by radial partitions, the septa, which stretch from base, column, and peristome to the œsophagus, dividing the peripheral part of the gastral space into small pockets, the radial chambers, connected below the end of the œsophagus with the central part. Above, these chambers continue into the tentacles. The tentacles therefore are outgrowths from the radial chambers and usually are equal in number to them. Besides the complete or primary septa which reach the œsophagus, there may be others incomplete in that they do not reach the œsophagus and belonging to secondary, tertiary or other series (fig. 203).

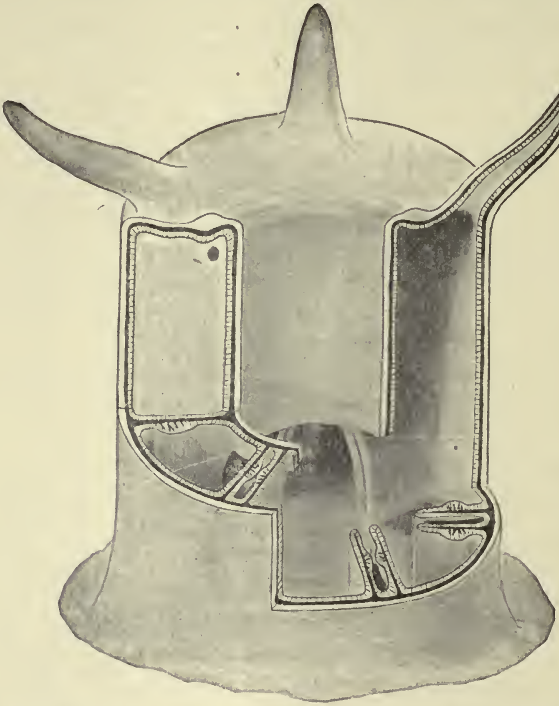


FIG. 200.—Stereogram of an Anthozoan (orig.). In the cut edges the ectoderm white, the entoderm blocked, the supporting layer black. The septa show the septal muscles, and the communication of the interseptal chambers with the œsophagus is seen.

The septa support a number of important organs: the mesenterial filaments, gonads, and muscles. The mesenterial filaments are thick strands of epithelium rich in glands and nettle cells, fastened like a hem on the edge of the septa. Since they are much longer than the peristomial-pedal length of the septa, they cause these latter to wrinkle and fold, thus strikingly resembling the mesenteries of the mammals. Lower down, in some species, the filaments become free and form long threads, *acontia*, rich in nettle cells which are protruded for defence either through the mouth or pores (*cinclides*) in the column. The gonads—only exceptionally hermaphroditic—lie inside the mesenterial threads as band-like folded thickenings (fig. 201, h^3). They arise as in the Scyphomedusæ from the entoderm, but early migrate into the mesoglœa of the septum (fig. 202, *o*). The eggs, when ripe, escape into the gastrovascular cavity by dehiscence. The young leave the parent at various stages of development, sometimes as planulæ (fig. 206, *A*), sometimes as young with tentacles.

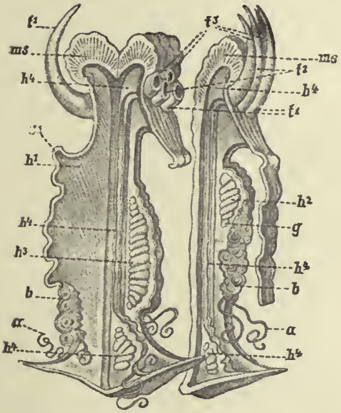


FIG. 201.

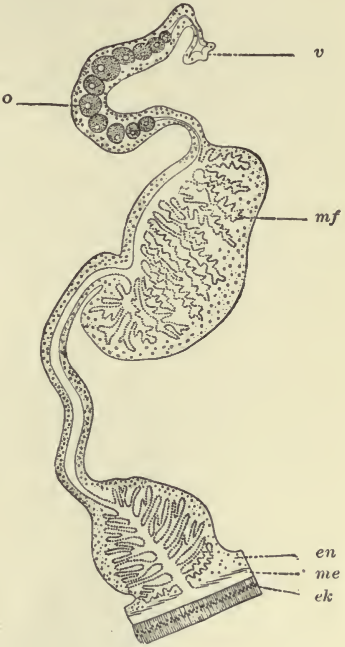


FIG. 202

FIG. 201.—Sections of *Cereus spinosus*, showing complete and incomplete septa. *a*, acontia; *b*, mesenterial filament; *c*, septal stoma; *g*, gonads; h^1, septa of first order with gonads; h^2—h^4, incomplete septa of second to fourth order; t^1—t^4, corresponding tentacles.

FIG. 202.—Section of septum of *Edwardsia tuberculata*. *ek*, ectoderm; *en*, entoderm; *me*, supporting layer; *mf*, septal muscle; *o*, ovary; *v*, mesenterial filament.

The muscles are very important, morphologically. Muscles and nerves occur in both ectoderm and entoderm; but while the nerves are best developed in the ectoderm, forming especially a thick subepithelial sheet of fibres and ganglion cells in the peristome, the muscles of the ectoderm are weakly developed and are confined to the peristome and the tentacles. The entodermal musculature is much stronger. At the oral end of the column is usually a strong circular (sphincter) muscle which by its contraction can draw the top of the column over the peristome. The septa also bear muscles, on one side running transversely, on the other longitudinally, the latter alone being strongly developed and producing marked ridges (fig. 202) on the septa.

In the Hexacoralla the septa are arranged in pairs, not only in being close to each other, but in having similar faces turned towards each other. The rule is (fig. 203) that in each pair the sides bearing muscle ridges are turned towards each other, but in two pairs lying in the sagittal axis these muscles are turned outward. From these relations these septa are called directives. It is however to be noted that in our common anemone, *Metridium*, occasionally three, more frequently but one pair of directives occur. The paired condition of the septa allows the recognition of two kinds of radial chambers; between the two of a pair is an intraseptal,

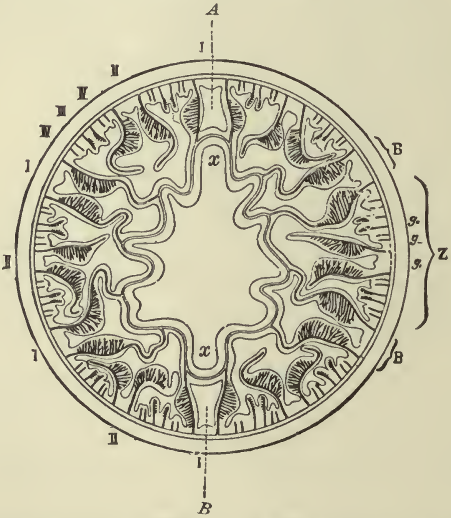


Fig. 203.—Transverse section of actinian (*Adamsia diaphana*) *AB*, plane of symmetry, a second lies at right angles. I–IV, septa of four orders.

between two pairs an interseptal chamber. New septa only appear in the interseptal chambers. At one time all Hexactinians have but six septa, a pair of directives and, right and left, four lateral septa. With growth, other septa of a secondary order may appear in the interseptal areas, giving six of these. And so with septa of the tertiary order. Irregularities however occur, and forms are found which have abandoned this sexfold plan and have assumed a plan of four or ten, but without altering the primitive conditions.

In the Octocoralla (fig. 204) the conditions are simpler, only eight septa being developed. These are disposed equally on either side of the œsophagus and may have (most octocorallans) all their muscles towards one end, or (*Edwardsia*, fig. 205, IV) may have the muscles of one pair reversed. It is to be noted that hexactinians pass through an *Edwardsia* stage. In *Cerianthus* new septa are always added at one end of the sagittal axis (fig 205, II), while in the extinct Tetracoralla (fig. 205, I), so far as one may judge from the hard parts, the septa have an arrangement with four as the basis.

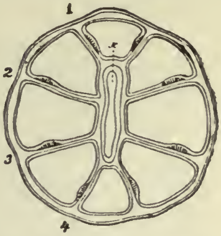


FIG. 204.—Transverse section of an Octocorallan (*Alcyonium*). *x*, siphonoglyphe; 1-4, septa of one side, with their muscles on one side, symmetrical with those of the other side.

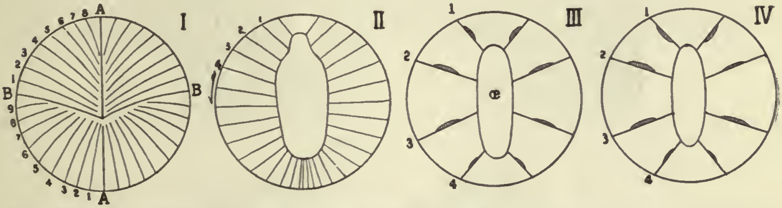


FIG. 205.—Arrangement of septa in various Actinozoa. I, Tetracoralla; II, *Cerianthus;* III, Octocoralla; IV, *Edwardsia.*

By far the greater part of the Anthozoa reproduce by budding as well as by eggs. Only rarely do the buds separate, but generally they remain connected with the mother to form a colony of hundreds or thousands of individuals. These are connected by an extensive cœnenchym or cœnosarc, consisting largely of mesoglœa, but having an outer coat of ectoderm and penetrated by a system of branching and anastomosing entodermal canals (fig. 206). On disturbance the polyps can quickly retract themselves into the cœnosarc.

The colonial Anthozoa have almost invariably a skeleton, secreted by the ectoderm and consisting either of calcic carbonate or of an organic horn-like substance. Sometimes the horn and lime alternate. One recognizes an axial and a cortical substance. The axial skeleton is confined to the deeper portions of the cœnosarc, while the cortical portions are formed by the polyps themselves and to a large extent (figs. 207, 208) repeat their complicated structure. Except in a few forms (*Fungia*) a theca is present; this is a calcareous cup, and from this usually extend inward calcareous partitions called, in distinction to the fleshy- or sarcosepta, the sclerosepta.

The theca arises by a fusion of sclerosepta. If this fusion takes place some distance inside the peripheral ends of the sclerosepta, the distal ends of these project on the outer surface as costæ. Still outside these may be a second cup, the *epitheca*. In the centre may occur a large calcareous column or several smaller ones, the *columella* (fig. 208). *Pali* are small

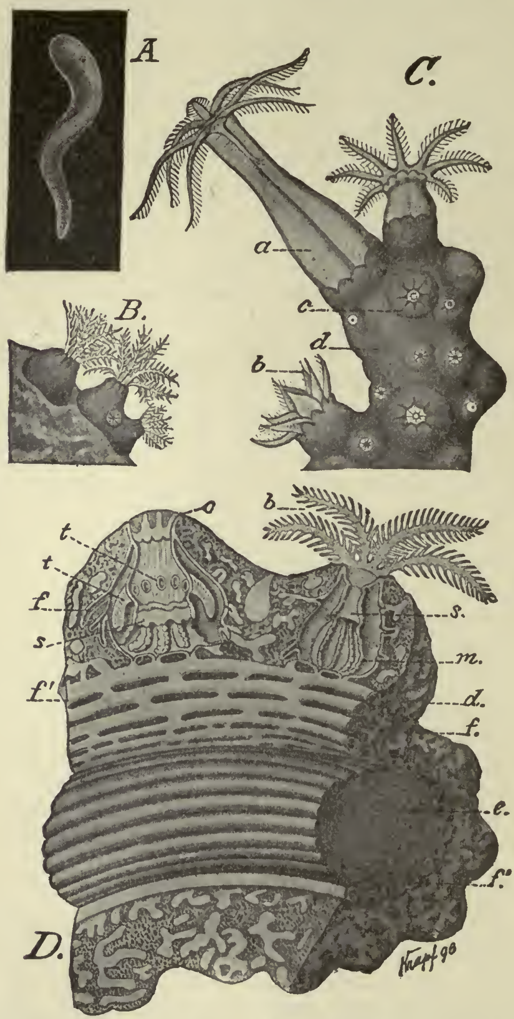


FIG. 206.—*Corallium rubrum*, red coral. (After Lacaze Duthiers.) *A*, ciliated young; *B*, young colony; *C*, part of colony with polyps in extension (*a*) and contraction (*c*); *d*, cœnosarc; *D*, stereogram of a branch; *b*, *c*, partly and completely retracted polyps; *d*, cœnosarc; *e*, skeletal axis exposed; *f'*, *f*, larger and smaller cœnosarcal canals; *m*, mesenterial filaments; *s*, œsophagus; *t*, retracted tentacles; *A*, greatly, *B*, *C*, *D*, slightly enlarged.

free particles between the inner ends of the sclerosepta and the columella, while *synapticulæ* are small projections connecting the septa. As the polyps grow they build the thecæ higher and higher and consequently draw out from the deeper portions, which may become cut off by horizontal partitions, the tabulæ. Such tabulæ occur in some Madreporaria, Octocorallans, and Millepores (p. 241) which were formerly united in a group Tabulatæ.

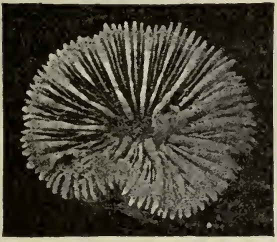


Fig. 207.

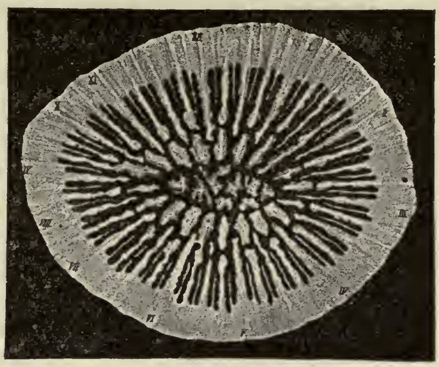


Fig. 208.

Fig. 207.—*Sclerophyllia margariticola.* (After Klunzinger.)
Fig. 208.—Section of coral of *Caryophyllia cyathus.* (After Koch.) Outside the theca, septa (I–XII) of first and second order, their pali and, in centre, columella.

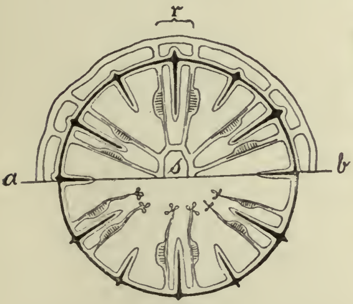


Fig. 209.

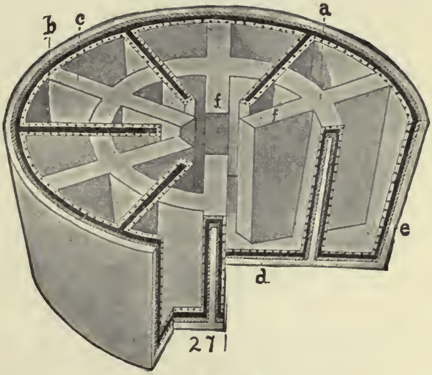


Fig. 210.

Fig. 209.—Diagrammatic section of the flesh and coral of a hexacorallan; above the line the section passes through the œsophagus, *s*; below the line it is lower down; *r*, directives; coral black.
Fig. 210.—Diagram of the relations of the coral to the polyp. (After Koch.) Ectoderm lined, mesoglœa black, entoderm dotted, coral white. *a*, theca; *b*, mesenteries; *c*, costæ; *d*, basal plate; *e*, external wall; *f*, sclerosepta.

It was once thought that the coral was a calcified portion of the soft parts and hence that sclerosepta were hardened sarcosepta etc. This has been disproved. The sclerosepta are formed in the radial chambers between the sarcosepta, and the theca inside and at some distance from the column, the outer surface of which secretes only the inconstant epitheca (fig. 209). From the above it would appear that the sclerosepta correspond in number to the sarcosepta, but this is not always the case. Thus the Helioporidæ, which on the grounds of the skeleton were regarded as Hexacoralla, are shown by the soft parts to be undoubted Octocoralla.

By means of their skeletons the Anthozoa produce large accumulations of carbonate of lime, the well-known coral reefs, on the bottom of the sea. These are formed by many species, the Madreporaria playing the most important rôle. When the reef reaches the surface it produces an island, the most noteworthy form being the atoll, a ring-like structure with a central lagoon. The origin of these atolls, as well as that of fringing and barrier reefs, was for a long time explained by Darwin's and Dana's theory of coral reefs. Later investigations, notably those of Mr. Agassiz, afford another explanation.

Order I. Tetracoralla (Rugosa).

Extinct forms from the paleozoic rocks with the parts arranged in fours (fig. 211). The present tendency is to regard them as modified Hexacoralla.

Order II. Octocoralla (Alcyonaria).

These forms, which have eight single septa, are externally recognizable by their feathered tentacles, eight in number (fig. 206).

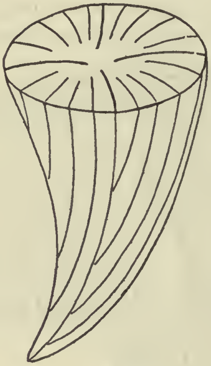


Fig. 211.

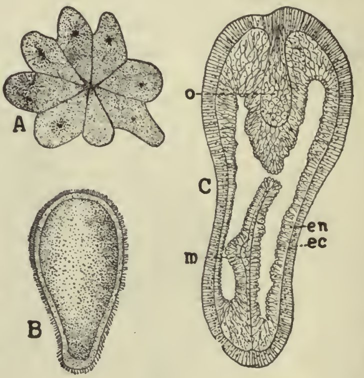


Fig. 212.

Fig. 211.—Diagram of septa in a tetracorallan. (Orig.)
Fig. 212.—Three stages in development of *Renilla reniformis.* (After Wilson.) *A*, cleavage of egg; *B*, planula; *C*, development of œsophagus; *ec*, ectoderm; *en*, entoderm; *m*, mesoglœa; *o*, œsophagus.

They occur in all seas from near the shore to great depths. In development there is a planula (fig. 212) in which the œsophagus arises as a solid ingrowth which becomes perforated later. The eight septa arise simultaneously. Usually colonies are formed by budding and a polymorphism may occur, some individuals which have reduced septa and lack tentacles, taking in water for the colony. Many are phosphorescent.

In the ALCYONIIDÆ (*Alcyonium*,* *Anthomastus*) an axial skeleton is lacking, but the flesh contains numerous calcareous particles, the sclerodermites. The sea pens, PENNATULIDÆ, have the basal part buried in the mud, the rest, expanded like a disc or feather, bears the polyps. An axial skeleton usually occurs in the stalk. *Pennatula*,* colder waters; *Renilla*,* warmer seas. The GORGONIIDÆ (sea fans, sea whips) have an axis of more firmness, which may be calcareous, and the colony may branch and the branches anastomose. Here belong, besides many tropical genera whose names end in '*gorgia*,' *Primnoa** of our colder waters; *Isis* of tropical seas, with skeleton of alternating calcareous and horny parts, and the precious coral (*Corallium rubrum*, fig. 206) of the Mediterranean, the fishing for which at Naples amounts yearly to half a million dollars. In the TUBIPORIDÆ, or organ-pipe corals, the separate polyps are enclosed in parallel tubes united at intervals by horizontal plates. The *Helioporæ* were long regarded as Hexacoralla because of their massive skeletons with six sclerosepta. The paleozoic *Syringopora* belongs near Tubipora, while the FAVOSITIDÆ resemble the Alcyoniidæ.

Order III. Hexacoralla (Zoantharia).

The simple tubular tentacles are highly characteristic of the Hexacoralla, as is the arrangement of the paired septa in sixes as described above. Yet there are exceptions to this rule. On the one hand is *Edwardsia* (common in our colder waters), in which there are sixteen or more tentacles and only eight septa (fig. 205), but which exhibits a condition through which the young actinians pass; on the other hand in the Zoantharia, Cerianthiæ, and Antipatharia the rule of six has undergone extensive modification.

Sub Order I. ACTINARIA (Malacoderma). The sea-anemones are mostly solitary, without skeleton; with numerous septa and tentacles. They occur in all seas from tide marks to the greatest depth. A few are free, but most are sessile. Except the colonial Zoantheæ all can creep by the pedal disc. Represented in our seas by *Metridium*, *Bunodes*, *Sagartia*, *Bicidium* (parasitic on *Cyanea*), *Halcampa*, etc. The Zoantheæ have two kinds of alternating mesenteries and the individuals of the colonies are usually incrusted with foreign matter. *Epizoanthus* lives symbiotically with hermit crabs (fig. 113).

Sub Order II. ANTIPATHARIA. Six pairs of septa and six (*Antipathes*) or twenty-four (*Gerardia*) simple tentacles; colony with a black horny axis and no calcareous skeleton. Simulate the Gorgonids.

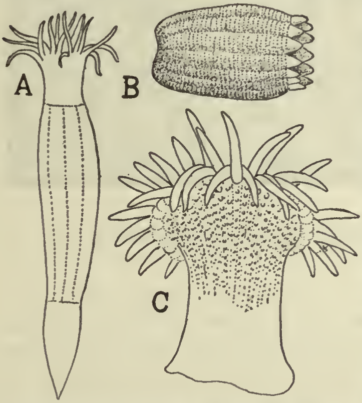


FIG. 213.—American sea-anemones. *A*, *Edwardsiella sipunculoides* (after Stimpson, *B*, *Bicidium parasiticum* (after Verrill), *C*, *Bunodes stella* (after Verrill).

Sub Order III. MADREPORARIA. This group, the richest in species of any, is characterized by the great development of the skeleton. Theca, septa, and usually columella and synapticuli are present, and frequently costæ as well. Solitary forms are few. Usually they form colonies, frequently of thousands of individuals, bound together by a cœnenchym extending from polyp to polyp over the surface of the coral. A colony arises from a single animal by continued fission or budding. When the division is not complete the animals may form long series with numerous mouths but with the other parts united, the result being that the surface of the coral is marked by long winding grooves—incompletely separated theca—with sclerosepta, as in the brain corals (fig. 215).

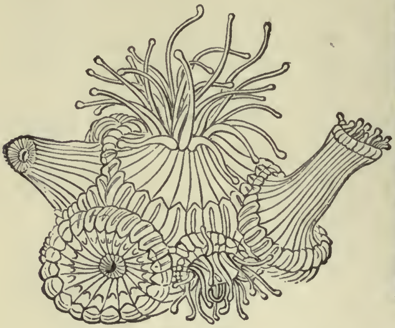


FIG. 214.

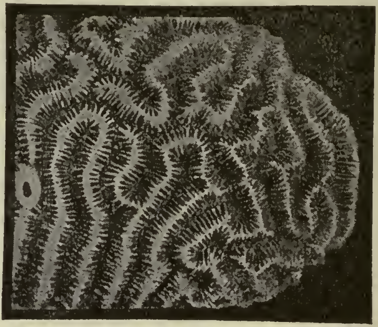


FIG. 215.

FIG. 214.—*Astrangia danae**; five polyps in various stages of expansion.
FIG. 215.—*Cœloria arabica.* (After Klunzinger.)

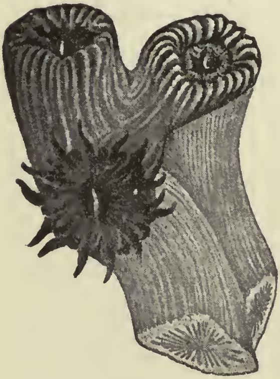


FIG. 216.

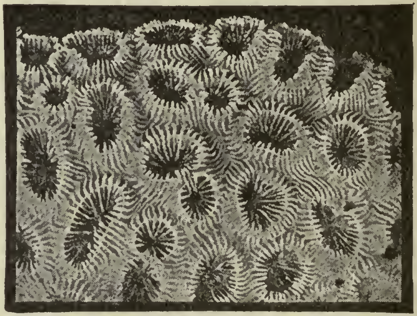


FIG. 217.

FIG. 216.—*Cladocora cæspitosa.* (After Heider.) Relations of coral and flesh.
FIG. 217.—*Favia cavernosa.* (After Klunzinger.)

Since but little is known of the soft parts, the classification of the Madreporaria is based upon the coral. Three sections of the sub order are recognized. (1) APOROSA, with compact skeleton. Some, like *Caryophyllia* (fig. 208) and *Sclerophylla* (fig. 207) are solitary. Others, like *Oculina*,* branch, and still others form compact masses. *Astrangia danae* (fig. 214), the only true coral in New England; *Astræa*, the brain corals (*Cœloria*, fig. 215, *Diploria*, *Manicina*); *Cladocora* (fig. 216), *Favia* (fig. 217).

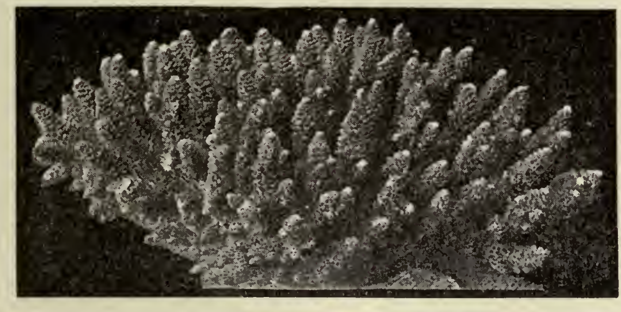


FIG 218.—*Madrepora erythræa*. (After Klunzinger.)

(2) FUNGIACEA, or mushroom corals, with no outer wall to the coral. Some are colonial, others (*Fungia*) are solitary. A sort of strobilation in development. (3) POROSA, with skeleton porous like a fine sponge. *Madrepora*,* deer's-horn coral (fig. 218), *Porites*, *Astroides*.

Class IV. Ctenophora.

The Ctenophores excel all marine animals, even the medusæ, in transparency and delicacy of tissues; many are so soft that a strong current tears them, and no attempts to preserve them have been successful. The body is almost always biradially symmetrical; *i.e.*, is divided by both sagittal and transverse planes into symmetrical halves. Since the longitudinal axis is usually longer than the others, which are generally equal, the body is usually oval or pear-shaped. In *Cestum* the sagittal axis is greatly longer, giving the animal the form of a band, whence the name 'Venus girdle.'

The bulk of the animal is composed of a soft jelly with connective-tissue cells, penetrated in every direction by polynucleate muscle cells branched at their ends and apparently innervated by special nerve cells. On the outer surface is a layer of ectoderm, while in the interior is a system of branched entodermal canals.

At the bottom of a depression (fig. 221B, *p*) at the aboral pole is a thickened patch of ectoderm, the sense body, which has considerable resemblance to an otocyst (fig. 222). The thick sensory epithelium forms a shallow groove, strong hairs which rise from the edge of the groove arch over it, enclosing a space to be compared to an incomplete vesicle. In the centre is a spherical

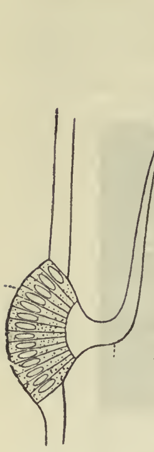


FIG. 219.

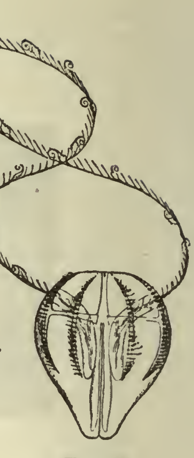


FIG. 220.

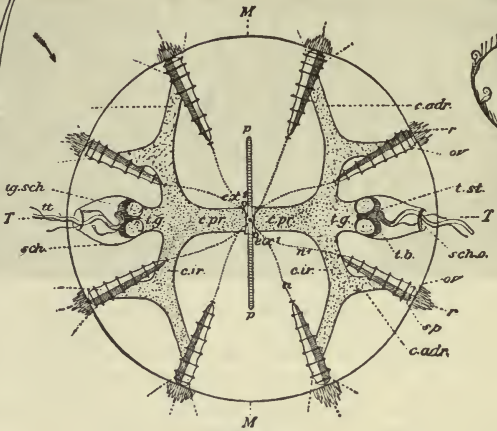

M
p
c.adr.
r
ov
t.st.
tg.sch
tt
T
c.x
c.pr.
c.pr.
t.g.
t.g.
T
sch.
ex
n
c.ir.
c.ir.
t.b.
sch.o.
ov
r
sp
c.adr.
p
M

FIG. 221*A*.

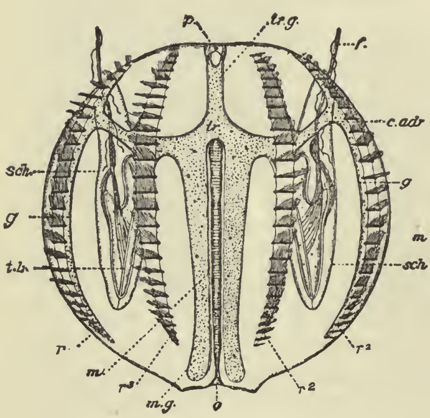

p
tr.g.
f.
tr.
c.adr
sch
g
g
sch
t.b.
r
m
r³
m.g.
o
r²
r²

FIG. 221*B*.

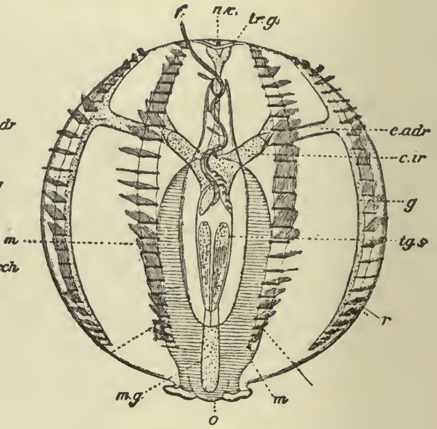

f.
n.c.
tr.g.
c.adr
c.ir
g
m
tg.s
r
m.g.
m
o

FIG. 221*C*.

FIG. 219.—Swimming plate and epithelial cushion. (After Chun.)
FIG. 220.—*Hormiphora plumosa*. (After Chun.)
FIG. 221.—*Pleurobrachia rhododactyla*. (After Chun.) *A*, aboral pole; *B*, front, *C*, side view. *MM*, sagittal axis; *TT*, transverse axis; *c.adr*, radial vessel; *c.ir*, interradial vessel; *c.pr*, right and left gastrovascular trunks; *ex*, opening of funnel vessel; *g*, subcostal vessel; *m*, 'stomach'; *mg*, paragastric canals; *n*, ciliated grooves; *nc*, sense body; *o*, mouth; *ov*, ovary; *p*, pole-plate; *r.r*^{3}, rows of combs; *sch*, tentacular pouch; *schs*, its aperture; *sp*, testes; *tb*, basis of tentacle; *tg. sch*, tentacular canal; *tr*, funnel; *trg*, funnel canal.

mass of otoliths, supported on four bundles of S-shaped agglutinate cilia. From these bundles of cilia eight bands of thickened epithelium, at first in pairs (fig. 223, *ws*), later diverging, pass to the oral pole (fig. 221, *r*). These meridional bands (so called from their course) consist in part of ciliated epithelium, in part of the characteristic 'combs' which are the locomotor organs, and which must be regarded as transverse rows of long agglutinated cilia. The combs (fig. 219) arise from thick epithelial ridges, transverse to the meridional bands, and are so far apart that the free edges of one comb overlap the base of the next like shingles. In consequence of their fibrous structure the combs are strongly iridescent and in motion cause a beautiful play of metallic red, blue, and green over the meridional bands. These combs act like oars and row the body about. Since the combs begin some distance from the aboral pole, they are connected with it by means of ciliated grooves following the line of the meridional bands. Experiment shows that the sense body is an organ of equilibration and of correlating the action of the different rows of combs.

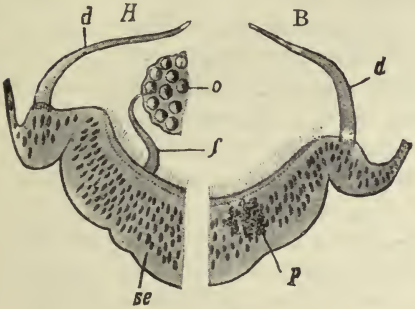


FIG. 222.

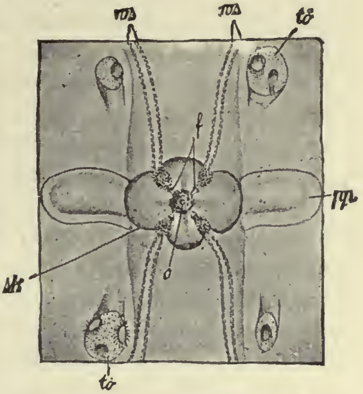


FIG. 223.

FIG. 222.—Section of sense body of *Callianira*. *A*, through the centre ; *B*, excentric ; *d*, roof of sensory groove ; *f*, support of otoliths, *o* ; *p*, pigment cell ; *se*, sensory cells.

FIG. 223.—Aboral pole of *Callianira bialata*. (From Lang.) *f*, supports of otoliths, *o* ; *pp*, pole plate ; *sk*, sense body ; *to"*, openings of gastral funnels; *ws*, ciliated bands.

The ectoderm gives origin to two more important organs, two pole fields and two tentacles. The pole fields (fig. 221, *p*; 223, *pp*) are two epithelial patches extending a short distance in the sagittal axis from the sense body and possibly are olfactory or taste organs. The tentacles arise, in the transverse axis, from the bottom of deep tentacular sacs, from which they project as long cords with numerous lateral branches, and into which they may be retracted. Tentacles and branches contain an axial muscle, while the ectodermal coating consists largely of adhesive cells. These are spherical bodies (fig. 224) covered with a very sticky granular secretion, and, like a *Vorticella*, supported on the end of a spiral stalk muscle. These are used in capturing prey.

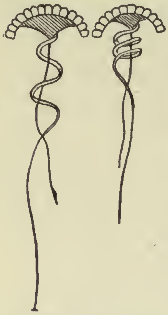


Fig. 224.—Adhesive cells of Ctenophora. (After Samassa.)

The ectoderm also forms part of the gastrovascular system. It turns inward at the mouth—situated at the lower end of the chief axis—and lines the large space commonly called stomach (fig. 221, *m*) but which corresponds to the œsophagus of the Actinozoa. At the aboral end of this stomach begin the true entodermal portions, the so-called funnels, and from them the canals distributed through the jelly to the various organs. Two (rarely four) funnel canals run to the aboral pole and empty (fig. 223, *to*) near the sense body; a second pair, the paragastric canals (fig. 221B, *mg*), which run parallel to the œsophagus, end blindly. The perradial canals (*c.pr*) proceed outward from the funnel, and besides giving off a canal to the tentacle (*tg*) each divides dichotomously twice, first into interradial and then into adradial canals, each of these last connecting with a meridional vessel running just beneath a row of combs, nourishing them as well as the gonads. The gonads consist of two bands, one male, the other female, running in that wall of the meridional vessel nearest to the combs. In spite of their position they are apparently ectodermal in origin.

These gonads are regular in distribution, those of two vessels which are nearest each other being of the same sex. The eggs and sperm pass out through the gastrovascular system.

The few species of the group are divided into the TENTACULATA, with tentacles, and the NUDA, without. To the first belong the CYDIPPIDÆ, with pear-shaped bodies (*Pleurobrachia* * on our coast, fig. 222), and *Hormiphora* (fig. 221); the LOBATÆ (*Mnemiopsis*,* *Bolina* *), with lobes; and the band-like CESTIDÆ (*Cestum*, the Venus girdle) of the warmer seas. The BEROIDÆ (*Beroe*, *Idyia* *), with wide mouth, belong to the Nuda. The small creeping forms, *Cœloplana* and *Ctenoplana*, are supposed by some to form a transition to the Turbellaria.

Summary of Important Facts.

1. The CŒLENTERATA (together with the Echinoderma) were formerly called Radiata because in most a radial form of structure is present; in the higher groups this can be transformed into biradial or even bilateral symmetry.

2. The Cœlenterata are sometimes called Zoophyta (animal plants), from their appearance and their attachment. In many the resemblance is heightened by their formation of plant-like colonies by fission and budding.

3. The name Cœlenterata was chosen because they have but one system of cavities, a simple or ramified digestive sac, representing at once the alimentary tract and the as yet undifferentiated body cavity.

4. This cœlenteric apparatus is called the gastrovascular system because its branches distribute nourishment to all parts and so perform the function of blood vessels.

5. The reproduction is either sexual or asexual, very frequently cyclical (alternation of generations).

6. The animals are provided with nerves, muscles, and sense organs and possess marked sensibility and mobility.

7. Especially characteristic are the tentacles and small nettling organs, the cnidæ, in special cells.

8. Nearly all histological differentiation proceeds from ectoderm or entoderm, since the mesoderm (mesoglœa) plays but a subordinate rôle and usually functions only as a support.

9. Four classes—Hydrozoa, Scyphozoa, Anthozoa, and Ctenophora are recognized.

10. In HYDROZOA and SCYPHOZOA there are usually two alternating generations, the sessile asexual polyp and the free-swimming sexual medusa.

11. The hydroid polyp and the craspedote medusa are characteristic of the HYDROZOA.

12. The hydroid polyp is a two-layered sac of ectoderm and entoderm, a supporting layer and a circle of tentacles. In the colonial forms there is usually a cuticular envelope, the perisarc, secreted by the ectoderm.

13. The craspedote medusa is bell-shaped, with smooth bell margin, its aperture partially closed by a diaphragm-like velum; the gonads are ectodermal.

14. The medusæ arise by lateral budding from the hydroid.

15. If the medusa remain attached to the parent as a sporosac,

alternation of generations is replaced by polymorphism; it can entirely disappear with the total loss of either hydroid or medusa.

16. The scyphostoma and the acraspedote medusa are typical of the SCYPHOZOA.

17. The scyphostoma differs markedly from the hydroid polyp in the presence of four longitudinal gastric folds or septa (tæniolæ).

18. The acraspedote medusa lacks a velum, has a lobed umbrella edge, gastral tentacles (phacellæ), and entodermal gonads.

19. The medusa arises from the polyp by terminal budding (strobilation).

20. Alternation of generations rarely is lost, and then only by suppression of the scyphostoma.

21. The ANTHOZOA have only one form, the coral polyp; it is distinguished from the hydroid polyp by the ectodermal œsophagus, the radial septa reaching the œsophagus; the well-developed mesoglœa and the gonads which, arising from the entoderm, early migrate into the mesoglœa.

22. Most Anthozoa are colonial and produce a skeleton usually of calcic carbonate, but sometimes of 'horny' substance.

23. The skeleton may be either axial or it may extend over the individual polyps (cortical skeleton).

24. The living Anthozoa are divided according to the number of septa into Octocoralla and Hexacoralla. To these are added the fossil Tetracoralla.

25. The *Hexacoralla* have numerous tubular tentacles and six, or a multiple of six, pairs of septa.

26. The *Octocoralla* have eight single septa and eight feathered tentacles.

27. The CTENOPHORA are always free-swimming and have a large mesoderm with numerous muscle cells.

28. Nettle cells are absent, and are replaced by adhesive cells.

29. Most characteristic are the eight meridional rows of 'combs' whose motions are controlled by a common organ, the sense body, constructed like an otocyst.

30. The digestive tract consists of an ectodermal œsophagus and a branching system of entodermal vessels.

PHYLUM IV. PLATHELMINTHES (FLATWORMS).

This group is well characterized by the name. With few exceptions (rhabdocœles, many trematodes) the nearly flat ventral surface and the slightly arched back are closely approximate and pass with a more or less sharp margin into each other. In many cases the ventral surface is distinguished by its lighter color. In all the bilaterally symmetrical body is composed of a solid parenchyma, a mass of connective tissue traversed by muscle fibres, in which the various organs—alimentary tract, nerves, excretory and reproductive organs—are imbedded. In the lower forms the digestive system is markedly like that of the cœlenterates (Actinozoa, Ctenophora) in that there is but a single opening and this leads by an ectodermal œsophagus (stomodæum) to the interior. In parasites the digestive tract may be lost. The skin is a one-layered epithelium, sometimes ciliated, sometimes protected by a thick cuticula. Inside this comes a muscular layer (fig. 225) in which longitudinal muscles are always present, and in addition frequently circular and oblique muscles, as well as those passing from dorsal to ventral surfaces. The nervous system (fig. 228) consists of a pair of ganglia ('brain') in front of (*i.e.*, above) the œsophagus and longitudinal nerves leading backwards from it. The excretory organs (fig. 226) are composed of a series of tubes, the protonephridia or 'water-vascular system,' which branch and ramify the parenchyma. In most the sexes are united in one individual and the reproductive organs take up considerable space. There is a small paired or unpaired ovary and *vitellaria*, usually paired and branched. The eggs arise in the ovary, and to these are added nourishment in the shape of cells (abortive ova) rich in yolk from

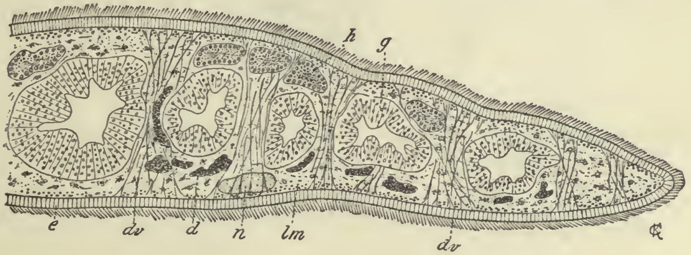


FIG. 225.—Transverse section (right half) of a Planarian. *d*, vitellaria; *dv*, dorsoventral muscle fibres; *e*, ectodermal epithelium with cilia; *y*, gastric diverticula; *h*, testicular follicles; *lm*, longitudinal muscles (dots, in section); *n*, lateral nerve cord.

the vitellaria. At the point where oviducts and yolk ducts unite a single egg cell together with several yolk cells are united into an oval body—the compound egg—protected by a shell secreted by special glands (fig. 227, *A*). This forms only an apparent exception to the rule that the egg is but a single cell, for the development shows that only the egg cell takes a direct part in the formation of the embryo and is the true ovum, while the yolk cells break down and furnish food to the growing embryo (fig. 227, *B*).

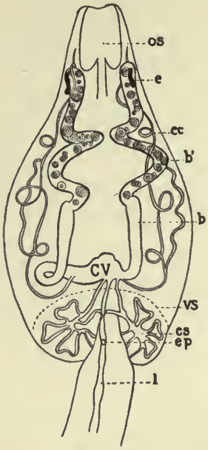


Fig. 226.

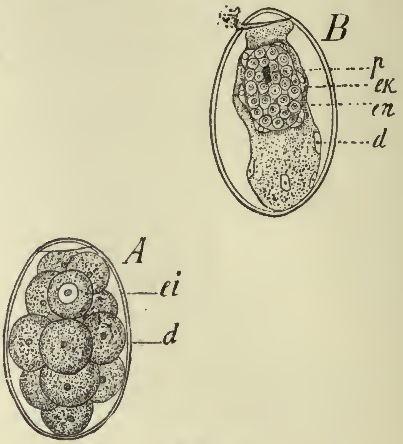


Fig. 227.

Fig. 226.—Excretory system of Cercaria. (After Albert Lang.) *b*, limb of bladder; *b′*, same with urinary concretions; *cc*, collecting canal; *cs*, canals of ventral sucker; *cv*, collecting vacuole; *e*, eye; *ep*, excretory pore; *l*, lumen of tail; *os*, oral sucker; *vs*, ventral sucker.

Fig. 227.—Eggs of *Distomum nodulosum*. (After Schauinsland.) *A*, before development; *B*, later, the yolk broken down. *d*, yolk cells; *ei*, egg cell; *ek*, ectoderm; *en*, entoderm; *p*, pigment spot.

Class I. Turbellaria.

The Turbellaria are small, only a few being measured by inches, while many are almost microscopic in size. The name Turbellaria has reference to the currents produced by the ciliated ectoderm which covers the body, the cilia arising from the single layer of columnar epithelial cells (fig. 58). This ectoderm serves at once for motion and for respiration. Most species are aquatic (fresh water or marine), only a few land planarians living in moist earth. In the water they either creep slowly over stones or plants on their ventral surface, or they swim freely. In swimming the larger species progress by undulations of the body, the smaller by means of the cilia.

The alimentary canal (fig. 228) consists only of œsophagus (pharynx) and mesenteron, the latter terminating blindly since no intestine or anus is present. The mouth is on the lower surface, at some distance from the anterior end, being occasionally in the middle or even behind the middle of the body (fig. 231). It leads into the muscular œsophagus, which is frequently enclosed in a special sheath and then can be protruded like a proboscis.

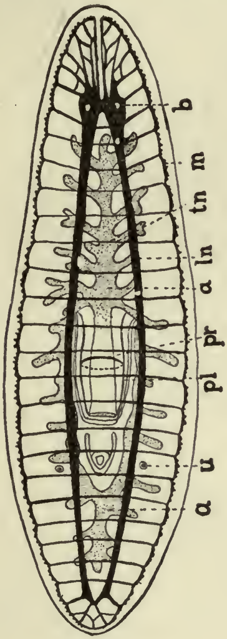


FIG. 228.

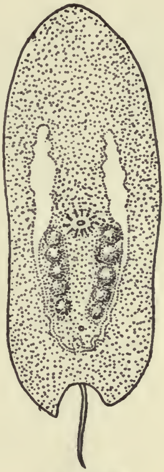


FIG. 229.

FIG. 228.—Digestive and nervous systems of *Syncœlidium pellucidum.* (After Wheeler.) *a*, alimentary tract; *b*, brain; *ln*, longitudinal (ventral) nerves; *m*, marginal nerve; *pl*, longitudinal nerve of pharynx; *pr*, ring nerve of pharynx; *tn*, transverse nerve; *u*, uterine ostium.
FIG. 229.—*Polychœrus caudatus.* (After Mark.)

The mesenteron, of entodermal origin, varies greatly in shape, its modifications being made the basis of division of the class into orders. In the Polycladidea there is a central portion from which numerous branched cæca are given off; in the Tricladidea there are three main trunks, each with lateral cæcal diverticula; while in the Rhabdocœlida the digestive tract is a simple rod-like sac, in some cases (Acœla) without internal cavity. The supra-œsophageal ganglia always lie at the anterior end of the body, which is most sensitive, and may be produced into feeler-like processes. This region usually bears two or more simple eyes, and in a few a single otocyst.

In many Turbellaria nettle cells, like those of the Cœlenterata, occur in the skin. Much more common are the rhabdites, small rods which arise in epithelial cells which sometimes project like glands into the mesoderm. Those rhabdites occur in the shiny tracks which the animals leave in creeping.

The hermaphroditic sexual organs (fig. 73) and the excretory system vary considerably in the separate orders and families. The eggs are usually very large and are fastened by a stalk to water plants. Many species form a sort of cocoon, containing a few eggs and numerous yolk cells. In the marine species a free-swimming larva (fig. 230) with lobe-like processes may hatch from the egg.

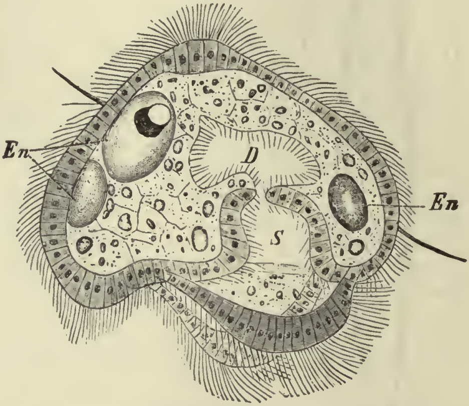


FIG. 230.—Larva of *Stylochus pilidium.* (From Korschelt-Heider, after Götte.) *D*, enteron; *En*, remains of entoderm cells; *S*, œsophagus.

This larva, by a metamorphosis, is converted into the creeping adult. Not infrequently besides the sexual asexual reproduction occurs. The Microstomidæ and some *Planariæ* are capable of transverse division, and, when well nourished, by rapidly repeated divisions will form chains of individuals arranged in a row, separation taking place gradually. For each posterior individual a new brain and a new œsophagus are formed (fig. 58). The Turbellaria possess the power, to a marked degree, of reproducing lost parts, which makes them favorites for regeneration experiments.

In a few Turbellaria there is a noteworthy condition of the digestive organs. The pharynx connects with an entodermal syncitium, a protoplasmic mass, without lumen, containing nuclei in which, as in the protoplasm of a protozoan, the food is digested. This entoderm is hardly marked off from the mesoderm, but it is a question whether these 'Acœla' are primitive or degenerate.

Order I. Polycladidea.

Marine species of considerable size, in which the digestive cæca spring from a central chamber. Species of *Leptoplana* and *Stylochus* on our shores. *Thysanozoon*, Europe.

Order II. Tricladidea.

Alimentary canal with three main trunks, an anterior unpaired and a pair of posterior branches, arising from the pharynx. These trunks bear lateral cæcal branches. Among the marine genera are *Bdelloura* * and *Syncœlidium* * (fig. 229) (parasitic on *Limulus*), *Gunda*,* *Polychœrus* * (fig. 229); in fresh-water occur *Dendrocœlum*,* *Planaria*,* and *Polyscelis*.* *Phagocata* * with divided pharynx. The land planarians (*Bipalium*,* 10 or 12 inches long) are tropical, but have been introduced into greenhouses in various parts of the country.

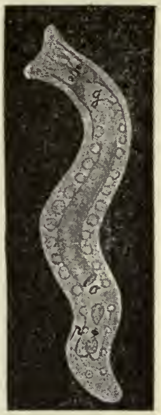


FIG. 231.—*Gunda lobata*. (After Schmidt.) *g*, cerebral ganglia, with eye-spots; *o*, mouth (entrance to long pharynx); *p*, genital pore with male organs behind, female in front.

Order III. Rhabdocœlida.

Small, even microscopic, in size, and recalling in habits and appearance the Infusoria; alimentary canal rod-like, without branches. *Monops* * and *Monoscelis*,* marine. The fresh-water MICROSTOMIDÆ reproduce almost exclusively by fission, so that sexual individuals are rare.

Class II. Trematoda.

These are exclusively parasitic, some living on the skin or gills (ectoparasites) or in the interior of other animals (entoparasites). In structure they are closest to the triclad Turbellaria, from which they are especially distinguished by characters the direct result of their parasitic life. Thus they have lost the cilia or these only appear in the aquatic larval stages. On the other hand they are armed with structures derived from the skin—suckers and hooks—for adhesion to the host. The suckers are shallow pits of columnar epithelium, lined with cuticle and furnished with a thick muscular layer which by its contraction increases the lumen of the sucker, the edges of which are closely applied to the host. At least one such sucker is present; if but one or two (entoparasites), one is at the anterior end (oral sucker) and surrounds the mouth, while a second larger sucker may occur near the mouth (fig. 232), but may be (*Amphistomum*) at the posterior end. In the ectoparasites there are a pair of anterior suckers near the mouth; at the posterior end a single sucker, or a number of suckers or hooks or both on a sucking disc (fig. 234).

Other results of parasitism are the weak development of sense organs and brain and a tendency to development of accessory ganglia near the adhesive organs. Eye spots (two to four) occur occasionally in the ectoparasitic species and in the larvæ of the entoparasitic, rarely in their adult condition. The alimentary tract is forked (fig. 233) and occasionally (fig. 232) has dendritic blind sacs. To parasitism may also be attributed the great development of the sexual organs, which at maturity fill a great part of the body. Their features may be seen in fig. 233. Two vasa deferentia pass forward from the testes (*h*), unite and form a seminal vesicle. The terminal portion of the united ducts can be protruded as a penis or cirrus, armed with retrorse hooks. It is usually enclosed in a 'cirrus pouch.' The ovary (*o*) is very small and produces small eggs, deficient in yolk; hence the vitellaria (*d*) are well developed. The ducts from these unite with the oviduct, producing the uterus (*u*), which receives the eggs, is much convoluted, and empties beside (in some species in a common antrum with) the male sexual opening. The first part of the uterus is called the ootype because here the eggs and yolk cells are formed into eggs (fig. 227) and

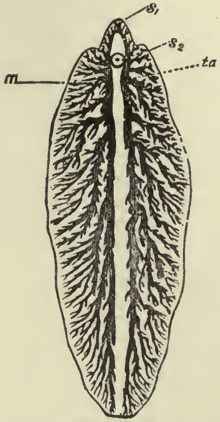


FIG. 232.

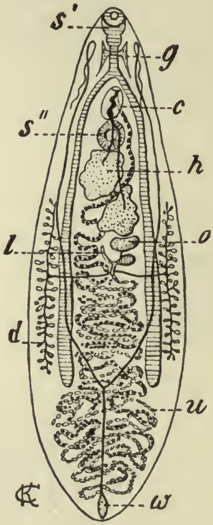


FIG. 233.

FIG. 232.—*Distomum hepaticum*, liver fluke. (From Boas.) *m*, cæca of *ta*, limbs of digestive tract; $s_1 s_2$, anterior and posterior suckers.

FIG. 233.—*Distomum lanceolatum*. *c*, cirrus, beneath it the opening of the oviduct; *d*, vitellaria, the ducts leading to the shell gland; *g*, ganglion; *h*, testes with ducts to cirrus; *l*, Laurer's canal; *o*, ovary, the shell gland behind it; *s'*, *s''*, anterior and median suckers, the pharynx and the bifurcated digestive tract leading from *s'*; *u*, uterus; *w*, terminal vesicle of water-vascular (excretory) system.

enclosed in a shell with a lid or cover. A second duct—Laurer's canal—goes from the oviduct to the dorsal surface. In many Polystomeæ the canal is double (fig. 234, *sw*) and is connected with copulation, but in the Distomes it is rudimentary or lacking and the opportunities are present for self-impregnation. Many Trematoda have a third canal—the vitello-intestinal duct—leading to the digestive tract.

The Trematodes fall into two great groups, the Polystomeæ, largely ectoparasites, and the Distomeæ, exclusively entoparasitic, the distinctions in parasitism being correlated with differences in structure.

Order I. Polystomeæ
(Monogenea, Heterocotylea).

Most Polystomes live on aquatic animals—usually fish, rarely crustacea, where they attach themselves especially to the thin-skinned and richly vascular gills. Since as ectoparasites they are exposed to more dangers, their adhesive organs are stronger than in the entoparasites. So while the anterior suckers are weakly developed, in some cases absent, the hinder end bears sometimes only a single sucker, but usually a large adhesive disc armed with many suckers and hooks. The transfer of Polystomes from one host to another presents few difficulties and hence the life history is without complications. The stalked eggs are attached near the mother and produce larvæ, which soon after hatching have the adult form (hence the name Monogenea).

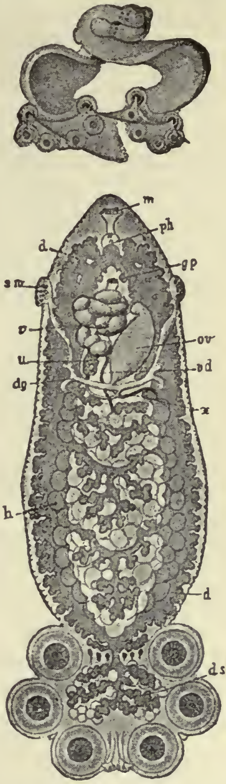


FIG. 234.—*Polystomum integerrimum.* (After Zeller.) Above two individuals in copulation; below a single animal enlarged. *d*, digestive tract, distended with blood; *dg*, yolk duct; *dst*, vitellarium; *gp*, genital pore; *h*, testicular vesicles; *m*, mouth; *ph*, pharynx; *ov*, ovary; *sw*, openings of the paired vaginæ; *u*, uterus; *v*, vaginæ; *vd*, vas deferens; *x*, vitello-intestinal canal.

The American species have been scarcely touched, hence most of our knowledge is of European species. *Gyrodactylus*, parasitic on the gills of the carp, is interesting, since it brings forth living young which, even before birth, produce a new generation in their interior. More striking is *Diplozoon paradoxum* (gills of Cyprinoids), which owes its name to the fact that, at the time of sexual maturity, two individuals become fused like Siamese twins (fig. 109). The young, described under the name *Diporpa*, escape from the eggs and only unite later. Each has a ventral sucker and a dorsal papilla. When they unite each of the pair seizes the papilla of the other with the sucker, and then the two grow together so that the male opening of one comes opposite the female opening of the other. *Polystomum integerrimum* of the frog (fig. 234) affords a transition to entoparasitism. At first it lives on gills of the tadpole, but at the time of metamorphosis it is forced to leave this place and pass, by way of the alimentary canal, to the urinary bladder. The TEMNOCEPHALIDÆ of warmer regions are partially ciliated, and have from four to twelve anterior tentacles and a posterior sucker. They are parasitic on crustacea, molluscs, and turtles, and are regarded by some as a distinct order. American genera of Polystomeæ are *Epibdella*, *Polystomum*, *Tristoma*, *Sphyranura*, *Microcotyle*.

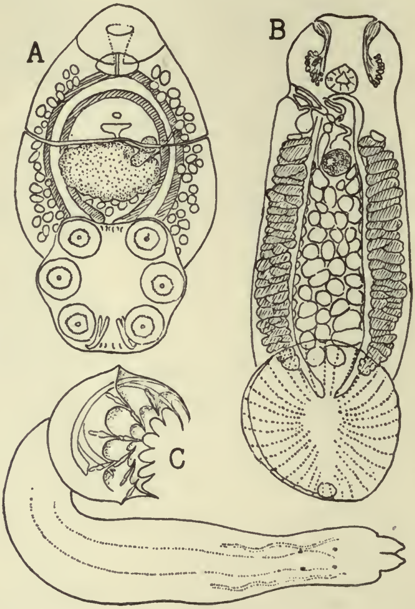


FIG. 235.—*A*, *Polystomum hassalli** (after Goto), from bladder of mud-turtle. *B*, *Acanthocotyle verrilli** (after Goto), from skate. *C*, *Gyrodactylus elegans* (after von Nordmann).

Order II. Distomeæ (Digenea).

The entoparasitic Trematodes occur largely in the digestive tract and its appendages; more rarely in blood-vessels, urogenital organs, and cœlom of vertebrates and other animals. As inhabitants of the dark they have, with few exceptions, lost the eyes, which appear in larval life, and not always then. Since not exposed to danger of being pulled from the host, they possess either the oral sucker alone (Monostomum) or this and a second ventral sucker, and only rarely other attaching apparatus. They are markedly separated from the Polystomes by their life history. The alternation of hosts necessitated by the endoparasitic life is complicated by an alternation of generations (better heterogony, p. 145) with

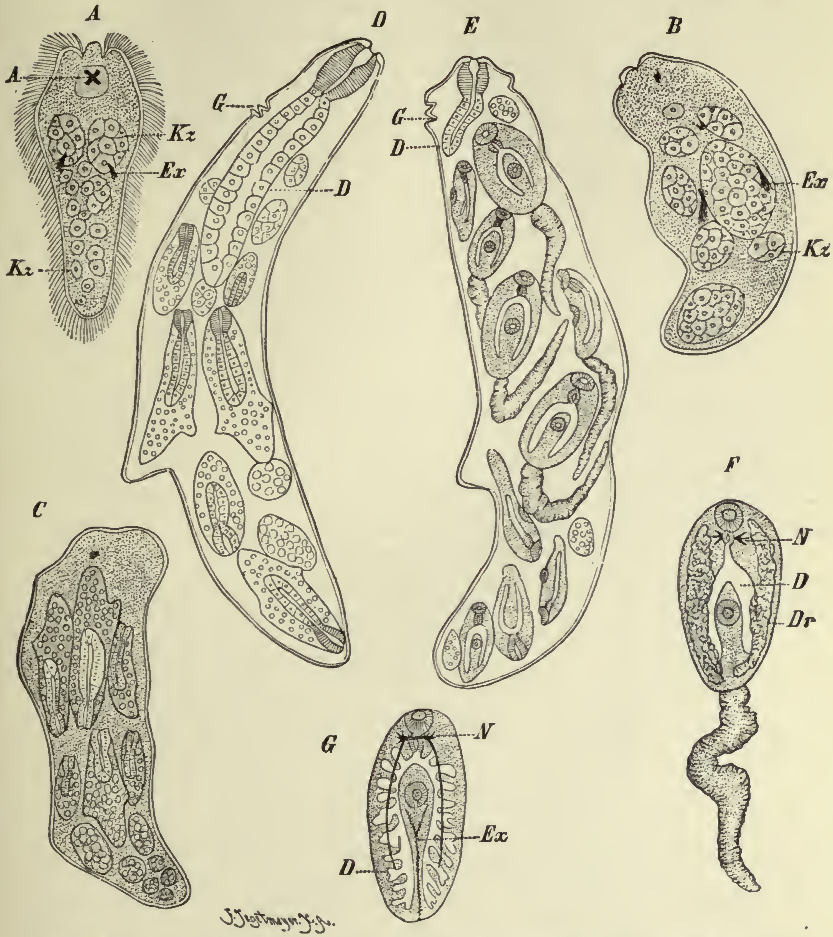


FIG. 236.—Development of *Distomum hepaticum*. (From Korschelt-Heider after Leuckart.) *A*, young larva; *B*, sporocyst from the lung of *Limnæa*; *C*, older sporocyst with rediæ; *D*, redia which has produced rediæ internally; *E*, redia with cercariæ; *F*, cercaria; *G*, encysted *Distomum*. *A*, eye spot; *D*, digestive tract; *Dr*, glands; *Ex*, ciliated lobules and main trunks of excretory system; *G*, birth opening; *Kz*, germ cells; *N*, nervous system.

metamorphosis. To illustrate this the history of *Distomum hepaticum* of the sheep is chosen (fig. 236).

The eggs leave the maternal uterus before embryonic development is begun, pass down the bile ducts and thence by the intestine to the exterior. They must come into water and remain here a while before the ciliated larva ('miracidium,' *A*) escapes by a lifting of the lid of the shell. This larva bores its way into a small snail (sp. of *Limnæa*), where it grows into a 'sporocyst' (*B*). The sporocyst, a muscular sac with protonephridia but lacking all other organs, produces in its interior eggs which develop into a second reproductive sac, the 'redia' (*D*). These are distinguished from the sporocysts by the possession of pharynx and a tubular intestine as well as a birth-opening for the escape of the young produced inside. According to the season these young are either 'cercariæ' (*F*), or several generations of rediæ may follow before the cercariæ appear. The cercariæ are adapted for an aquatic life, since each has, besides the characteristic organs of a *Distomum* (genitalia excepted), a strongly vibratile tail. The cercariæ escape from the snail, swim about in the water until the tail drops off, when they encyst on water plants. When these encysted young are eaten by sheep along with the vegetation, infection follows.

In general it can only be said of the life history of other Trematoda that the miracidia must penetrate a mollusc, and that the different species have many modifications: (1) Ordinarily development begins in the maternal uterus. (2) Many miracidia are naked or only partly ciliated. (3) In many species the miracidia only hatch when the egg is taken into the stomach of a snail along with food. (4) Very frequently the cercaria passes from the water into a new host (mollusc, arthropod, or vertebrate) and becomes encysted here. In such cases there are three hosts in the cycle. (5) On the other hand the history may be simplified, as when the sporocyst in the snail produces directly 'cercariæ without tails' (*i.e.*, small *Distoma*), which only need to be eaten by the definitive host to reach the sexually mature condition. (6) It is doubtful if the sporocyst may be omitted and the miracidia develop directly into redia.

As the adjacent scheme shows, the typical development is distributed among three hosts by the intercalation of a second aquatic interval. It consists of two generations; one extends from the fertilized egg to the sporocyst, the second begins with the unfertilized egg of the latter and develops, through the cercaria and the encysted *Distomum*, into the sexually mature individual. There is no sexual reproduction by fission or budding, rather an alternation of sexual and parthogenetic generations or heterogony. Columns *a* and *c* show how the history may be simplified and complicated.

Best known of the Distomeæ are the following: *Distomum* (*Fasciolaria*) *hepaticum*, the liver fluke (fig. 232), about the size and shape of a pumpkin-seed. It lives in the bile-ducts of sheep, cows, pigs, etc., and rarely (twenty known cases) of man. It stops up the ducts and causes a disease known as 'liver rot,' generally resulting in death. The history as described above shows why sheep pastured in moist places are subject to the disease, and why wet seasons are times of epidemics. Thus in the rainy year of 1830 about one and a half millions of sheep were killed in England; in 1812, 300,000 in the neighborhood of Arles, France. This species is frequently accompanied by *D. lanceolatum*, less than half an inch in length (fig. 233).

DEVELOPMENT OF DISTOMEÆ.

(*a*) Simple			(*b*) Ordinary			(*c*) Complicated		
Generation I	Larva	Water	Generation I	Larva	Water	Generation I	Larva	Water
	Sporocyst	Host I Mollusc		Sporocyst, perhaps also redia	Host I Mollusc		Sporocyst	Host I Mollusc
						Generation II	Redia	"
Generation II			Generation II	Cercaria	Water	Generation III	Cercaria	Water
	Encysted Distomum	Host I		Encysted Distomum	Host II		Encysted Distomum	Host II
	Sexually Mature Distomum	Host II		Sexually Mature Distomum	Host III		Sexually Mature Distomum	Host III

Bilharzia hæmatobia is a human parasite, most common in hot climates, and especially so among the Fellahin of Egypt. The sexes are separate. The male, half an inch long, by inrolling of the ventral side (fig. 237) forms an incomplete canal (canalis gynæcophorus) in which the more slender female usually lies. These united worms occur in the portal vein and connected vessels. They follow these vessels in either direction and lay their eggs in the mucous membrane of the ureters and urinary bladder, as well as in liver and intestine. The suppurative sores of the urinary tract cause albuminuria or, by hemorhage, hæmaturia. Diagnostic of the disease is the presence of the eggs, each with a spine, in the urine. Several other species occur in man, among them *D. carnosum** and *D. westermanni** in

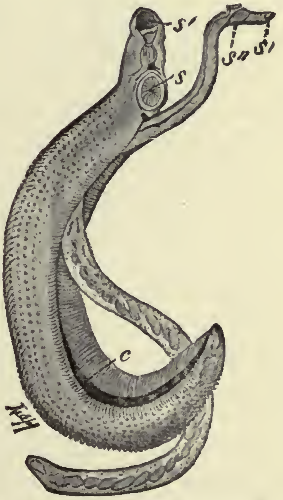


FIG. 237.—*Bilharzia hæmatobia.* Female in the gynæcophoral canal (c) of the male; *s'*, *s''*, anterior and posterior suckers.

America. Other species occur encysted in man, two (*D. ophthalmobius* and *Monostomum lentis*) in the capsule of the lens and in the lens itself. The genus *Amphistomum* is common in the intestine of Ungulates, one species, *A. hominis*, occurring in man. With few exceptions the adult stages of all Distomes occur in vertebrates, the larval stages in molluscs. Aquatic birds are very apt to be infested with them, and "it may be of interest to *gourmets* to know that the trail of a woodcock largely consists of distomic Trematodes."

Class III. Cestoda.

The majority of the cestodes, and especially those of the human intestine, are distinguished from the similarly entoparasitic trematodes in a striking manner. But the boundaries between the two groups disappear in certain forms like *Archigetes*, *Caryophyllæus*, and *Amphilina*, parasitic in lower vertebrates or invertebrates and which are now assigned to the trematodes, now to the cestodes. The most important character of the cestodes is that as a result of their parasitic life they have lost the last traces of an alimentary canal, and are nourished by the juices or the partially digested food of the host, since the fluid nourishment is taken in through the skin into the body parenchyma. It is a disputed question whether the cuticula of the surface is penetrated with pores for this purpose.

Two other characters are so striking that they are among the first thought of. (1) The differentiation of two developmental stages, the bladder worm, or cysticercus, living chiefly in parenchymatous organs (muscles, liver, brain), and the sexually mature animal, living as a parasite in the alimentary tract; (2) the division of the body of the adult into different parts, the head or scolex, and following this a series of joints or proglottids. Since this last feature holds for all human tapeworms and hence for the best known species, the following description begins with these typical forms.

The sexually mature tapeworm or strobila (fig. 238) consists of a single scolex in front, and behind this follow in a single row the proglottids. The number of these last varies from smaller forms (*Tænia echinococcus*, fig. 252) with three or four to several hundreds or even several thousands, a fact which speaks for the enormous size of some species. The proglottids are derivatives of the scolex, from the hinder end of which they become separated by a kind of budding. This explains the well-known fact that the body is not rid of the tapeworm, so long as the head remains in the host. It also explains the peculiar shape of the worm, which is almost thread-like in front, increasing posteriorly to a broad band, whence the common name. At first the proglottids are small; they increase by individual nourishment to considerable size, and separate from the hinder end of the chain and live separately when a certain measure of development is reached. For example, the young proglottids of the human tapeworm, *Tænia solium,* are 0.5

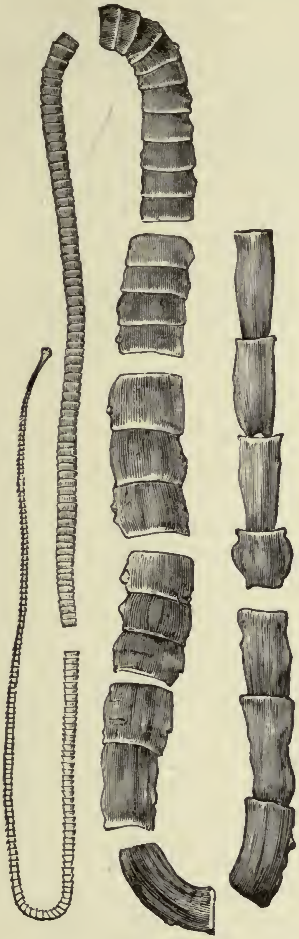


FIG. 238.

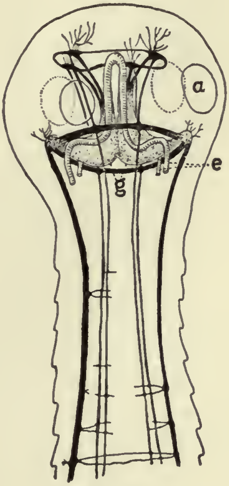


FIG. 239.

FIG. 238.—*Tænia saginata.* (From Boas, after Leuckart.) Head with series of proglottids taken from various regions of the strobila.

FIG. 239.—Nervous system of *Monezia.* (After Tower.) *a*, suckers; *e*, excretory tubes; *g*, cerebral ganglia. Nerves black.

mm. broad and 0.01 mm. long; the ripe proglottids at the end are elongate oval, 5 mm. broad and 12 mm. (half an inch) long.

Head and proglottids have certain common characters. Their connective-tissue parenchyma contains numerous spherical concretions of lime, and consists of cortical and medullary substance. The first contains to a marked degree the muscles, the latter the other organs. Nerves and water-vascular system extend through the whole length of the worm. In the head is the paired cerebral ganglion of the flatworms (fig. 239), sometimes fused to a single mass by the great development of the commissure or partially concealed by accessory parts connected with attachment (fig. 242). From the brain two principal nerves run backwards, usually near the edges of the proglottids (fig. 244, *N*). The water-vascular (excretory) system begins with a capillary network richly provided with flame cells. It extends through head and proglottids; usually four main trunks are present, two being less developed and it is possible are sometimes absent. The two chief trunks are frequently connected by a cross-trunk on the hinder margin of each proglottid (fig. 244). The system opens on the posterior edge of the last proglottid, but accessory mouths may occur on other proglottids.

The scolex and proglottids are distinguished by the facts that the proglottids contain the sexual organs, while the scolex bears the anchoring apparatus, for the latter has, besides producing proglottids, to fasten the worm in the intestines. Most important of the adhesive organs are the suckers (acetabula); less important are the hooks, which, in numbers, are either arranged in a circle or are borne on protrusible and retractile probosces (fig. 240–242).

When a circle of hooks is present it is on the anterior end and is moved by a special apparatus, the rostellum. This is a plug of complexly arranged muscles (fig. 242) which can arch and flatten the central area. In many species the arching is increased by a muscular sheath, the flattening by retractors. Each hook has its point outwards and its base with two roots, one of which rests on the rostellum; the protrusion of the rostellum forces the points outwards into the mucous membrane of the intestine. In some *Tæniæ* without the circle of hooks (*T. saginata*) the rostellum is replaced by a sucker-like depression. Since the rostellum arises in development from a similar cup, it may be a modified apical sucker, but it is doubtful how far comparisons may be made with the oral sucker or the alimentary tract of the trematodes.

The sexual organs are hermaphroditic and are present in numbers equal to those of the proglottids, so that these were formerly regarded as sexual individuals of a colony, each with its own reproductive apparatus. Two types must be recognized. In the one the presence of vitellaria and the separate openings of uterus and vagina recall the conditions in trematodes, while in the second

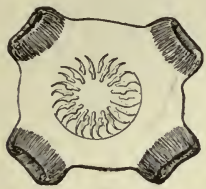


FIG. 240.

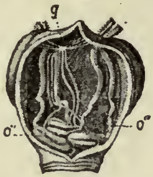


FIG. 241.

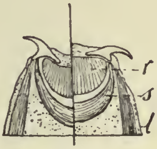


FIG. 242.

FIG. 240.—Apical view of head of *Tænia solium.* (From Hatschek.)
FIG. 241.—Head of *Tetrarhynchus viridis.* (After Wagner.) Dissected to show the internal parts of the proboscides (*o*) and the ganglion (*g*).
FIG. 242.—Schema of action of rostellum. On the right the hooks are exserted for adhesion, on the left retracted. *r*, rostellum; *s*, sheath; *l*, longitudinal muscles.

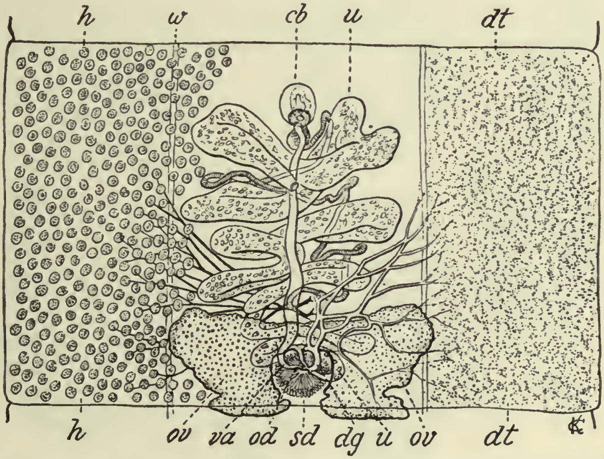


FIG. 243.—Proglottis of *Bothriocephalus latus.* (After Sommer.) Right only vitellarium, left only testes. shown. *cb*, cirrus sheath opening with the vagina; *dg*, vitelline duct; *dt*, vitellarium; *h*, testes; *od*, oviduct; *ov*, ovary; *sd*, shell gland; *u*, uterus; *va*, vagina; *vd*, vas deferens (dark-lined); *w*, excretory canal.

the uterus ends blindly and the vitellaria are modified into a small albumen gland. Since vagina and vas deferens almost always open together, self-impregnation is possible. Besides cross-fertilization of separate proglottids has been seen. The general features of the two types may be made out from figures 243 and 244, reference

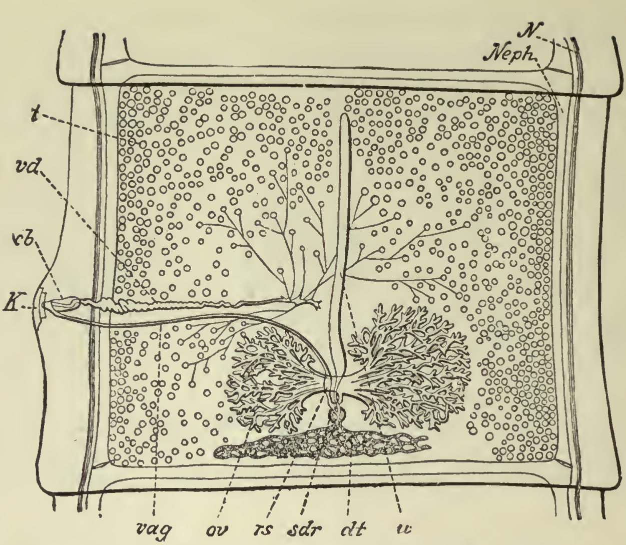


FIG. 244.—Proglottid of *Tœnia saginata*, near maturity. (After Sommer.) *cb*, cirrus sheath; *dt*, vitellarium; *k*, genital pore; *N*, nerve cord; *Neph*, excretory canal; *ov*, ovary; *rs*, receptaculum seminis; *sdr*, shell gland; *t*, testes; *u*, uterus; *vd*, vas deferens.

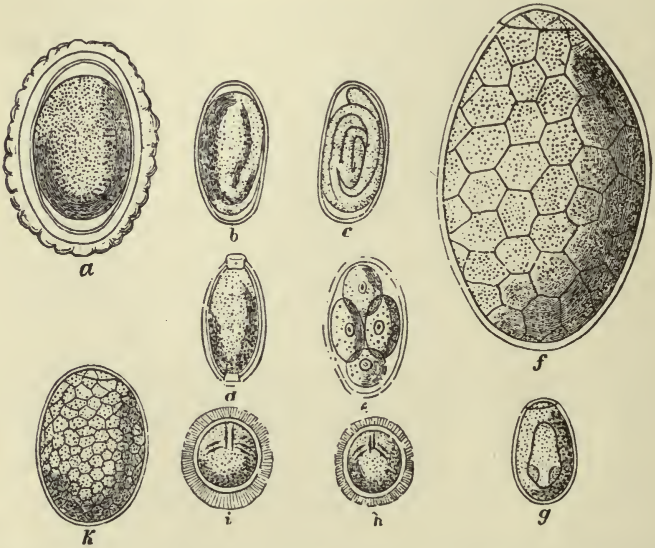


FIG. 245.—Eggs of parasites from the human intestine, enlarged 400 diameters. (From Leuckart.) *a*, *Ascaris lumbricoides*; *b*, *c*, *Oxyuris vermicularis*; *d*, *Trichocephalus dispar*; *e*, *Dochmius duodenalis*; *f*, *Distomum hepaticum*; *g*, *Dist. lanceolatum*; *h*, *Tœnia solium*; *i*, *T. saginata*; *k*, *Bothriocephalus latus*.

being made to the description of the organs in the trematodes (p. 272).

The difference in the sexual apparatus has its influence on the peculiarities of the egg (fig. 245). In *Bothriocephalus* it is large (*k*), has a tough shell with a lid, and encloses a small egg cell with numerous yolk cells. The eggs of *Tænia* (*h*, *i*) are small, with a layer of albumen and a delicate shell which is lost early. It is replaced by an embryonic shell, a radially striped envelope secreted by the embryo in a somewhat advanced stage. It is in this condition that one usually sees Tænia eggs.

A further consequence is a difference in development. In most Bothriocephalidæ, as in the Trematoda, the egg must enter the water for its further development. Here a ciliated oval larva escapes which contains a six-hooked larva (*oncosphæra*, fig. 246).

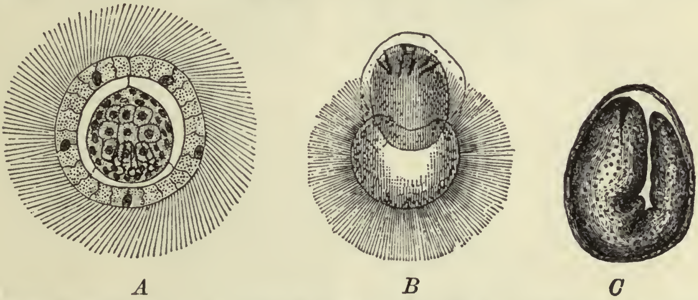


Fig. 246.—Development of *Bothriocephalus latus* (From Leuckart.) *A*, ciliated larva; *B*, same with escaping six-hooked larva; *C*, young encysted *Bothriocephalus*.

The ciliated envelope is temporary and is cast off like the ciliated coat of the trematode larva. The six-hooked larva in some unknown way enters a fish, becomes encysted (pleurocercoid) in muscles or viscera, and changes directly into the head of a *Bothriocephalus*. This on being taken, in feeding, into the intestine of the proper host develops into the adult.

The longer and better known history of the *Tænias* differs considerably. The distinctions are early recognizable, since the six-hooked larva lacks the ciliated envelope but is enclosed in its homologue, the embryonic shell already alluded to. Since this envelope cannot open of itself, the young must be freed from it by its digestion in the stomach of the proper intermediate host. Thus the eggs of *Tænia solium* must pass into the stomach of the pig (they are taken by admixture of the food with embryos contained in fæcal matter) and after being freed from their shell in the stomach the larvæ with their six hooks bore through the intestinal wall and migrate, using the blood-vessels in their course, into the muscles, or more rarely other organs. Here they develop into bladder worms (cysticerci). In this they become oval and secrete a cyst to which, as a foreign body, the pig adds an envelope of connective tissue. The cysticercus blastema grows through increase of cells, but more by the infiltration of serous fluid, so that it becomes distended into a delicate translucent vesicle. So abundant can this be that in *T. solium* the microscopically small embryo can grow in three or four months to the size of a bean or pea; in other species as large as a hen's egg. By invagination the wall of the bladder produces the blastema of the scolex (fig. 247, *c*). This has at first a sac-like shape, but soon increases in length, its growth being confined by an envelope, the receptaculum (*d*), so that it is bent.

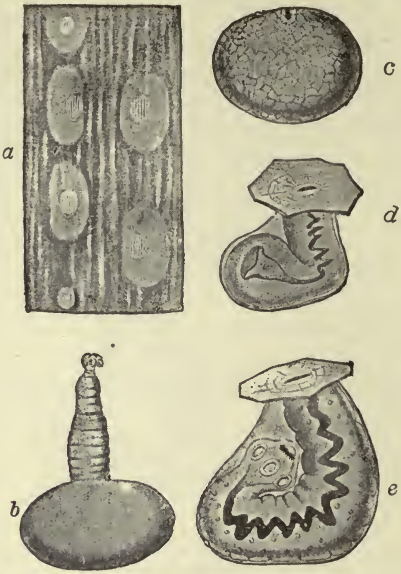


Fig. 247.—Structure and development of the cysticercus (C. cellulosæ of *Tænia solium*). *a*, measly meat, natural size; below an escaped cysticercus; *b*, cysticercus, with exserted scolex, enlarged; *c–e*, development of the scolex, more enlarged; *c*, young cysticercus with blastema of scolex (above) and water-vascular net; *d*, *e*, different stages of scolex in receptaculum, the cysticercal wall mostly removed.

At the apex of this blind sac arises the characteristic armature of the scolex which makes it possible to say what tapeworm will come from the cysticercus. Thus in *T. solium* there are four suckers and a crown of hooks. These parts are at first inverted and only come to their definitive position on the outside of the scolex when the latter is protruded as one would turn out the finger of a glove. The further development follows when the cysticercus is taken into the stomach of the new host. When man, for instance, eats infected ('measly') pork, the cysticerci are freed by action of the digestive juices and later the scolex is everted. The embryo passes to the intestine, becomes attached and, surrounded by nourishment, begins to grow, the bladder remaining attached to the hinder end, and soon the formation of proglottids begins in the middle piece connecting the bladder with the scolex. So rapid is the growth that in ten or twelve weeks *Tœnia solium* begins to set proglottids free.

In cases where the bladder reaches a considerable size it has the power of producing more than a single scolex. The bladder of *Cœnurus cerebralis*, which lives in the brain of sheep, produces hundreds of scolices. The number is even greater in *Tœnia echinococcus*, in which the bladder increases by budding for some time, and by the formation of numerous daughter bladders produces marked tumors in the liver of man and domestic animals, before the formation of scolices begins. In the interior of each daughter vesicle appear a number of brood vesicles, each of which produces numbers of scolices, so that from a single six-hooked embryo thousands of scolices can arise (fig. 253). This extreme case stands in contrast to others which connect with the development of *Bothriocephalus*, in which the cysticercus is replaced by a cysticercoid (fig. 248). Here there is no infiltration and the scolex is closely enclosed by an envelope comparable to the bladder wall.

All of this is of importance in the correct conception of the development of a tapeworm, which was earlier believed to be a complicated alternation of generations; the bladder to be a stage which by endogenous budding produced scolices; the scolex, in turn, a stage which by terminal budding produced the sexual animals, the proglottids, and the tapeworm itself a chain of individuals, a strobila. This view, so easy to learn, so easily explaining the development, contains two errors. The bladder is not an independent generation, but only the precocious hinder end of the scolex. The tapeworm is not a colony, but a single animal; the proglottids are not individuals, but specialized parts of a single whole. This view is confirmed by a comparison with other forms. The Caryophyllæidæ (fig. 249) are single bodies, the anterior end elongate and taking the place of the scolex, while the broader hinder part contains a single hermaphroditic apparatus. In the Ligulidæ the body is still unjointed, but has increased in length and contains numerous sets of sexual organs. This duplication of the reproductive apparatus explains the appearance of proglottids.

Family 1. CARYOPHYLLÆIDÆ (Cestodaria). Cestodes without acetabula, simple sexual apparatus, scolex and proglottis not differentiated. Distinguished from trematodes by absence of digestive tract. Larval stages in invertebrates, adults nearly always in fishes. *Caryophyllœus* (fig. 249) in the intestine of cyprinoids; *Amphilina* in body cavity of sturgeon; *Archigetes* in annelids (*Sœnuris*).

Family 2. Ligulidæ. No acetabula; numerous sexual organs, but no proglottids. The immature stages in the body cavity of fishes, the adults in the intestine of birds. *Ligula.*

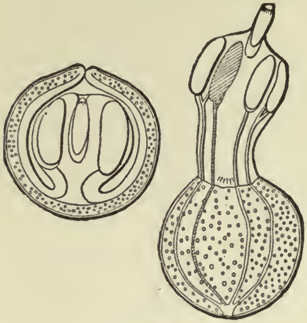


Fig. 248

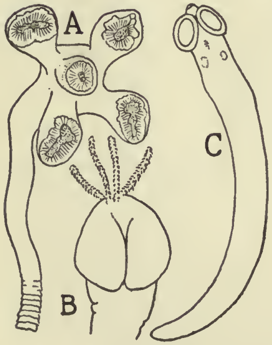


Fig. 250.

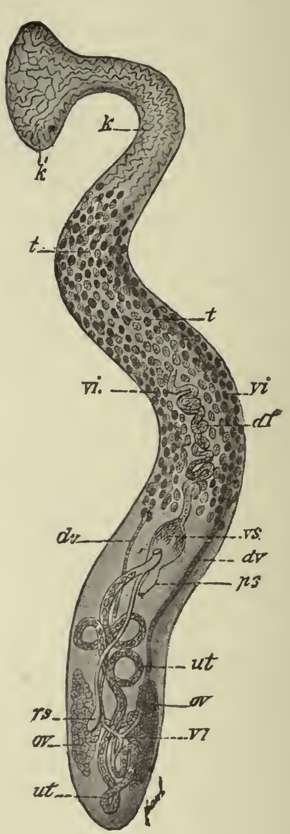


Fig. 249.

Fig. 248.—Cysticercoid in invaginated and extended condition from *Arion ater*. (From Hatschek.)

Fig. 249.—*Caryophyllœus mutabilis.* (After M. Schultze.) *df*, vas deferens; *dv*, vitelline duct; *k*, scolex; *ov*, ovaries; *ps*, penis; *vs*, vagina with receptaculum seminis; *t*, testes; *ut*, uterus; *vi*, vitellarium; *vs*, vesicula seminalis. The connexion of vagina with the crossing point of genital duct, vitelline duct, and uterus is lacking in the figure.

Fig. 250.—Tapeworms of fishes. (After Linton.) *A*, *Echinobothrium variabile**; *B*, *Rynchobothrium bisulcatum**; *C*, *Tetrabothrium.**

Family 3. Tetrarhynchidæ. With scolex and proglottids, the head with four protrusible hooked probosces (fig. 241). Immature and mature stages in fishes. *Tetrarhynchus*, *Rynchobothrium.**

Family 4. Tetraphyllidæ. Head with four very mobile suckers, often armed with hooks. *Echinobothrium* * (fig. 250), *Acanthobothrium.**

Family 5. BOTHRIOCEPHALIDÆ Scolex and proglottids present; head spatulate with two sucking groves on the narrower sides. Most interesting is *Bothriocephalus latus* (fig. 251), the largest tapeworm which occurs in the human intestine (also dogs and cats), and which may reach a length of forty feet and consist of over four thousand proglottids. As has been outlined above, the pleurocercoid occurs in fishes, and man acquires the parasite by eating uncooked fish. It is especially abundant in Russia, the eastern provinces of Prussia, and in Switzerland. It is rare in America and occurs most frequently in immigrants. Other species occur in man in Greenland (*B. cordatus*) and China (*B. mansoni*).

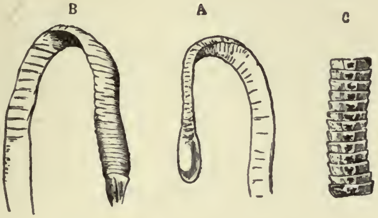


FIG. 251.—Head and ripe proglottids of *Bothriocephalus latus*, the head showing the sucker at the angle, the proglottids the marking produced by the uterus.

Family 6. TÆNIADÆ. With scolex and separable proglottids; the scolex always bears four suckers and in many a rostellum with a circle of hooks (fig. 252). In the proglottids the vitellarium is replaced by an albumen gland; the uterus is cæcal, and the genital pore occurs usually laterally in the proglottids, alternating right and left, rarely only on one side (*Hymenolepis*, *Anoplocephalus*). It is rarely doubled in a proglottid (*Dipylidium*, *Moniezia*). Intermediate stage a cysticercus or cysticercoid. The human tapeworms are grouped here together, but are subdivided accordingly as the sexual animal or the cysticercus has been found in man.

A. *Tæniæ* sexually mature in the human intestine. Most noticeable are *Tænia solium* and *T. saginata*, the differences between which are shown in fig. 252 and the following table. It is to be noticed that, in spite of the lack of hooks, the stronger suckers render *T. saginata* more difficult to expel. *Tænia solium*, as the table shows, is not rare in the cysticercus stage in man and occurs sometimes in places, like the brain and eyes, where it causes severe injury. These cases are in part explained by lack of cleanliness in the food, which may contain eggs, but it is possible through internal infection; pieces of the worm passing the pylorus and entering the stomach, where they are digested, setting the embryos free.

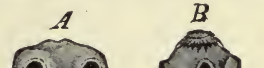


FIG. 252.—Head and ripe proglottid of (*A*) *Tænia saginata* and (*B*) *T. solium*.

	Head	Number of Proglottids	Uterus	Length (*a*) of the worm and (*b*) of the ripe proglottids	Character of Cysticercus	Occurrence of Cysticercus
Tænia solium	With rostellum and circle of hooks (26 in 2 rows); 4 weak suckers	800-900	Each side with 7-9 large branched pouches	*a.* 10 feet, *b.* 9-11 mm. long, 6-7 mm. broad	6-20 mm., with abundant fluid	In pigs, occasionally in muscles, brain, and eyes of man, rarely in other mammals
Tænia saginata	No rostellum; no hooks; 4 strong suckers	1200-1300	Each side with 20-30 delicate little branched pouches	*a.* 20 to 25 feet and more, *b.* 18-20 mm. long, 5-7 mm. broad	4-8 mm., tough, with little fluid	Cattle

Many other *Tæniæ*, which are common to other mammals, occur occasionally in the human intestine. In mice and rats occur *T.* (*Hymenolepis*) *murina* and *T. diminuta* (= *leptocephala*). The first (identical with *T. nana*) has recently been very abundant in human intestines in Italy. The worm, an inch or two long, may occur in thousands and cause severe injury. This species may develop without an intermediate host; the eggs taken into the stomach pass the cysticercoid stage in its walls and thence to the intestine to become adult. *T. diminuta* (= *flavopunctata*), which has insects for its intermediate host, has been described from man. Other species occur in the tropics.

B. Forms passing the cysticercus stage in man. Besides the cysticercus cellulosæ of *T. solium* that of *T. acanthotrias* (possibly identical with *T. solium*) has been found in man. More frequent and of more importance to the physician is the cysticercus of *Tænia echinococcus* (fig. 253), which lives as an adult in the dog, and is easily overlooked on account of its size. It is at most 5 mm. ($\frac{1}{5}$ inch) long and consists of a scolex and three or four proglottids. The scolex bears four suckers and hooks on the rostellum. When the eggs are taken into the human stomach, as may easily happen by stroking and kissing infected dogs, the embryos are set free and wander into liver, lungs, brain, or other organs and produce here tumors which, in the case of the liver, may weigh ten or even thirty pounds. This extraordinary size is explained by the formation of daughter bladders (echinococcus) described above. Echinococci are more common in cattle, sheep, and swine than in man.

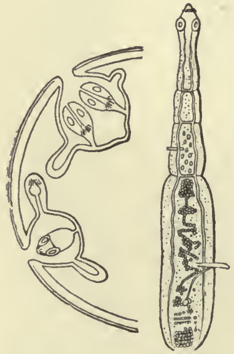


FIG. 253.—*Tænia echinococcus.* (After Leuckart.) Right sexually mature; left a part of an echinococcus with two brood capsules and their scolices.

Common *Tæniæ* of domestic animals are in the horse *Anoplocephala plicata* (4 to 30 inches), *A. perfoliata* ($\frac{1}{2}$ to 3 inches), *A. mamillana* ($\frac{1}{2}$ to

2 inches); in ruminants, *Moniezia expansa* (usually 7 feet, sometimes 30 feet or more), often fatal, *M. denticulata* (1 to 5 feet), the most common tapeworm of cows; in dogs, *Tænia marginata* (cysticercus in sheep and swine), *T. serrata* (cysticercus in rabbits), *T. echinococcus* (above), *T. cœnurus* (cysticercus in brain of sheep, causing the disease called 'staggers'), *Dipylidium cucumerina* (most common, larva in the dog-louse, *Trichodectes*); in the cat, *Tænia crassicollis* (cysticercus in mice). Several species occur in domestic birds, one (*Drepanidotænia infundibuliformis*), causing epidemics among chickens.

Class IV. Nemertini.

Most nemerteans are of appreciable size, some reaching a length of a yard or more (*Lineus longissimus* 90 feet !), and yet they are so contractile that a specimen of our *Cerebratulus lacteus*, which can extend itself to fifteen feet, can retract to two. Nemerteans are rare in fresh water or moist earth, but are most abundant in the sea, where they burrow through the mud or lie rolled up beneath stones. Many are noticeable for their bright colors. Their systematic position is a problem. Frequently they are included in the Plathelminthes, but the presence of an anus, of distinct vascular system, and the higher organization in other respects renders such a position doubtful.

Like some flatworms they have a solid parenchyma bounded externally by a ciliated ectoderm rich in mucus cells, and inside this at least two muscular layers, which, when but two are present, are an outer circular and an inner longitudinal layer. They differ from all other Plathelminthes in having a complete alimentary tract, beginning with a ventral anterior mouth and continuing as a straight tube, with, usually, paired diverticula, to the vent at the posterior end of the body (fig. 254).

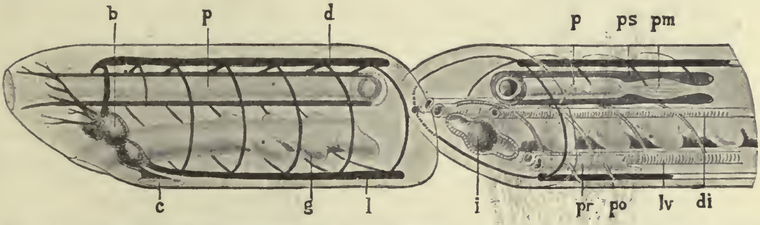
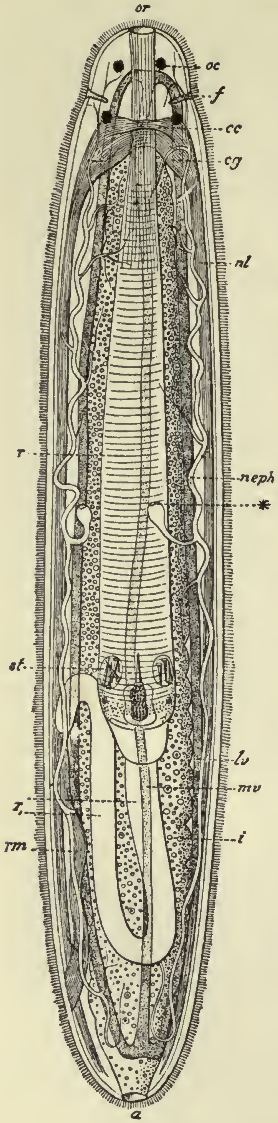


FIG. 254.—Diagram of Nemertean (orig.). *b*, brain; *c*, ciliated pit; *d*, dorsal nerve trunk; *di*, dorsal blood-vessel; *gc*, gastric cæca; *i*, intestine; *l*, lateral nerve trunk; *lv*, lateral blood-vessel; *p*, proboscis retracted; *pm*, proboscis muscles; *pn*, protonephridial tube; *po*, its opening; *ps*, cavity of proboscis sheath.

Especially diagnostic is the proboscis, which lies dorsal to the alimentary tract and usually opens separate from the mouth. The



proboscis is a muscular tube closed at one end and at rest is infolded like the finger of a glove inside a closed sac, the proboscis sheath, which extends far back in the body. Its tip is bound to the posterior end of the sheath by a retractor muscle. By contraction of the sheath the proboscis is everted, while it may be retracted again by the muscle. Nettle cells are not uncommon in the proboscis wall, while in some forms (the older Enopla) the effectiveness of the organ is increased by the presence of a dart-like stylet at the tip (reserve stylets occur on either side, fig. 255), and at the base of the stylet is the opening of a poison sac.

The blood-vascular system consists of a pair of lateral tubes connected by transverse loops, and in most forms a third tube is present lying between the intestine and the proboscis sheath. The excretory system consists of two tubes lying close beside the lateral blood-

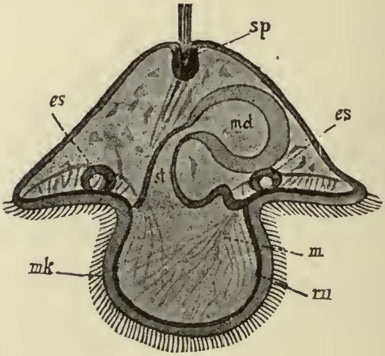


FIG. 255.

FIG. 256.

FIG. 255.—Young *Tetrastemma obscurum*. (From Hatschek, after M. Schultze.) *a*, anus; *cc*, dorsal commissure; *cg*, cerebral ganglia; *f*, ciliated grooves; *i*, digestive tract: *lv*, lateral, *mv*, dorsal blood-vessel; *neph*, water-vascular tubes; *nl*, lateral nerve; *oc*, eye spot; *or*, proboscis pore; *r*, proboscis; r_1, glandular hinder portion of proboscis; *rm*, retractor of proboscis; *st*, stylets; *, opening of excretory system.

FIG. 256.—Pilidium larva. (From Lang, after Salensky.) *es*, invaginations which later give rise to the nemertine skin; *m*, oral lobes; *md*, archenteron; *rn*, ring nerve; *sp*, apical plate; *st*, œsophagus; *mk*, ciliated band.

vessels and connecting with branches terminating in flame cells, while they open separately to the exterior by one or several openings.

The central nervous system (in some forms still in the ectoderm) consists of a supraœsophageal brain of a paired ganglia, from which nerves run to the proboscis and two lateral cords united on the ventral side by numerous transverse commissures. Connected with the brain, either directly or by means of a short nerve, are the cerebral organs or ciliated grooves, pits placed on the sides of the head. These, formerly regarded as respiratory, are now considered sense organs. Tactile organs and simple eyes are widely distributed; otocysts are very rare.

As a rule the nemertines are diœcious, the gonads forming a row of lateral sacs, alternating with the intestinal blind sacs and opening dorsally. The development is sometimes direct, but usually a metamorphosis occurs in which a larva, the pilidium (or a reduced form of it, Desor's larva), appears. The pilidium is a gelatinous helmet-shaped larva with right and left below a pair of lappets (fig. 256). The margins of lappets and helmet are ciliated, while at the top a bundle of longer cilia project from a thickened patch of ectoderm, the apical plate, which apparently functions as a central nervous organ. Inside is the simple cæcal archenteron, the mouth (blastopore) opening between the lappets. By a complicated process of growth and infolding this mesenteron becomes enclosed in its own skin, produced from four inpushings (*es*); an anus is formed, and at the time of metamorphosis the worm thus produced escapes from the rest of the pilidium, which quickly dies.

Order I. Protonemertini.

Nervous system outside the muscles; no stylets in the proboscis; mouth behind brain. *Carinella.**

Order II. Mesonemertini.

Nervous system in the muscles; mouth behind brain; no stylets. *Cephalothrix.**

Order III. Metanemertini.

Nervous system in the parenchyma inside the muscles, mouth in front of brain; proboscis as a rule with stylets. *Geonemertes** and some species of *Tetrastemma*,* terrestrial. *Amphiporus** (numerous eyes), *Nectonemertes.** *Malacobdella*,* leech-like with posterior sucker, parasitic in lamellibranchs.

Order IV. Heteronemertini.

Body wall with several muscular layers, the nervous system in the muscles; mouth behind brain; proboscis unarmed. *Lineus*,* *Micrura*,* and *Cerebratulus* * (*Meckelia*) on our coast, with cerebral organs. *Eupolia.*

Summary of Important Facts.

1. The PLATHELMINTHES are bilateral animals of flattened form whose nervous system consists of a supraœsophageal ganglion and lateral nerve trunks; the excretory system of branched water-vascular tubes (protonephridia).

2. The TURBELLARIA are the most primitive; the Trematoda and Cestoda have descended from them.

3. The Turbellaria are ciliated externally. They have no anus and no circulatory system. The digestive tract consists of ectodermal pharynx and entodermal stomach, the latter many-branched in the *Polyclads,* with three main branches in the *Triclads*, and rod-like in the *Rhabdocœles.*

4. Polyclads and Triclads are often united under the name *Dendrocœla.*

5. In the parasitic TREMATODA the cilia are entirely lost or confined to the larval stages. Hooks and suckers are present for attachment to the host; several in the ectoparasitic forms; only one or two suckers in the internal parasites.

6. In the *Distomiæ* there occur heterogony and alternation of hosts. From the egg arises a sporocyst, always parasitic in molluscs, from the parthenogenetic eggs of which develop cercariæ which become encysted Distomiæ in the second host, sexual Distomiæ in the third.

7. Best known of the *Distoma* are *D. hepaticum* and *D. lanceolatum* (rare in man, common in sheep) and *D. hœmatobium* in the portal vein of man in warm climates.

8. The CESTODA are characterized by the entire absence of digestive tract, and usually by the existence of scolex and proglottids.

9. The scolex is the organ of attachment, and as such is provided with suckers and frequently with hooks. It also produces the proglottids by terminal budding.

10. The proglottids contain an hermaphroditic sexual apparatus.

11. The eggs produce a six-hooked embyro which must pass into an intermediate host. This is accomplished either by taking the eggs in passively with the food, or the embryo must pass into the water, where it infects fishes.

12. The embryo, in the intermediate host, becomes encysted and changes directly to a scolex (pleurocercoid) or into a bladder worm (cysticercus) which produces internally one or more scolices.

13. The scolex is freed from its cyst when taken along with food into the stomach of the proper host, and then acquires the capacity of development into a tapeworm.

14. In man occur as cysticerci *Tænia echinococcus* (adult in dog) and *T. solium;* as adults *Tænia solium* (cysticercus in pigs), *T. saginata* (cysticercus in cattle), and *Bothriocephalus latus* (pleurocercoid in fish).

15. The NEMERTINI are distinguished by a complete alimentary canal with anus, and a proboscis dorsal to the digestive tract.

PHYLUM V. ROTIFERA (ROTATORIA).

The aquatic wheel animalcules, or Rotatoria, are among the smallest Metazoa, and can be distinguished from the Infusoria, which they resemble in habits, only by the microscope. The body is divisible into three regions, head, trunk, and tail. The trunk is covered by a tough cuticle into which head and tail can be retracted. The tail or 'foot' is often composed of rings which can be telescoped into each other and which by their superficial resemblance to segmentation formerly led to the association of the rotifers with the Arthropoda. The last tail ring often bears a pair of pincer-like stylets which together with adhesive glands enable the animal to adhere to objects. The head has the most delicate cuticle and is expanded in front to a trochal disc, an apparatus of varying appearance, which is surrounded by a ring of cilia of use in swimming and also in directing food to the ventral mouth. The

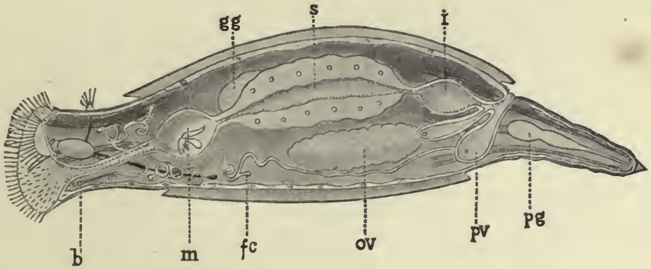


FIG. 257.—Diagram of rotifer. (After Delage et Herouard.) *b*, brain; *fc*, flame cell; *gg*, gastric gland; *i*, intestine; *m*, mastax; *ov*, ovary; *pg*, pedal gland; *pv*, pulsating vesicle of excretory system; *s*, stomach.

alimentary canal consists of œsophagus, mastax (chewing stomach), glandular stomach, and intestine; all except the mastax cilated. The mastax bears two chitinous jaws (trophi), which in life are in constant motion and comminute the food. The cerebral ganglion lies above the œsophagus, with which simple eyes and peculiar sense organs, the cervical tentacles, are frequently connected. The usually single ovary and the paired protonephridia empty into the posterior part of the alimentary canal, which thus becomes cloacal in character. For a long time males were unknown until Dalrymple discovered that these are much rarer and smaller 'dwarf males,' and that they have a much simpler structure (fig. 258, *B*). Usually the alimentary tract is reduced to a solid cord in which the testes are imbedded.

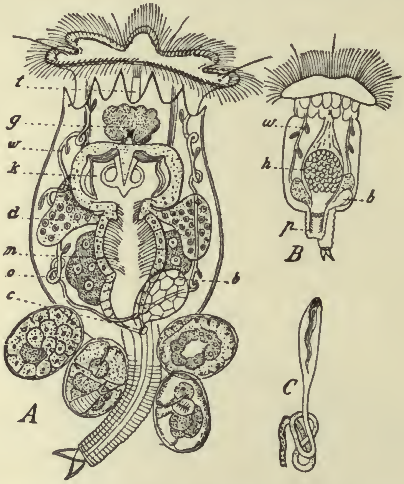


Fig. 258.—*Brachionus urceolaris*. *A*, female with four eggs in various stages; *B*, male; *C*, 'flame' from protonephridia, greatly enlarged; *b*, urinary bladder; *c*, cloacal opening; *d*, gastric glands; *g*, ganglion, with eye; *h*, testis; *k*, mastax; *m*, stomach; *o*, ovary; *p*, penis; *t*, tentacle; *w*, protonephridia.

The Rotifers have two kinds of eggs, large winter eggs enclosed in a thick shell and smaller thin-shelled summer eggs. The latter develop parthenogenetically and by their numbers and rapid growth subserve the distribution of the species. The winter eggs require fertilization, and have a long resting period, thus serving to tide over periods of cold or drought. The adult animals can withstand a certain amount of desiccation; and they are often found in damp moss or in eave troughs in a sort of sleep from which they are awakened by water.

In structure the Rotifiers are much like the trochophore type of embryo of annelids and molluscs to be described later. They must hence be regarded as extremely primitive forms, connected at once with the ancestors of these groups, and, as shown by nervous system and excretory organs, with the flatworms as well. Most species are cosmopolitan and inhabitants of fresh water. Many species in America. Near the Rotifera may be placed the fresh-water GASTROTRICHA (*Ichthydium*, *Chætonotus*) and the marine ECHINODERIDÆ, forms which are little understood.

PHYLUM VI. CŒLHELMINTHES.

The Cœlhelminthes are distinguished from all the forms which have gone before by the presence of a body cavity, separating the outer body wall from the intestine. This cavity is the cœlom, but whether it be homologous in different groups, *e.g.* nematodes and annelids, is not settled. The body muscles are developed from the outer (parietal) epithelial wall of the cœlom and hence are 'epithelial muscle cells' (figs. 259, 260). The excretory organs connect the body cavity with the outer world and hence are nephridia (earlier called segmental organs, *cf.* fig. 69). Internally they begin with a ciliated funnel, the nephrostome, and continue as long coiled tubes expanding just before the outer end to a kind of bladder. The sexual apparatus is simple. The gonads (fig. 260, *o*) are

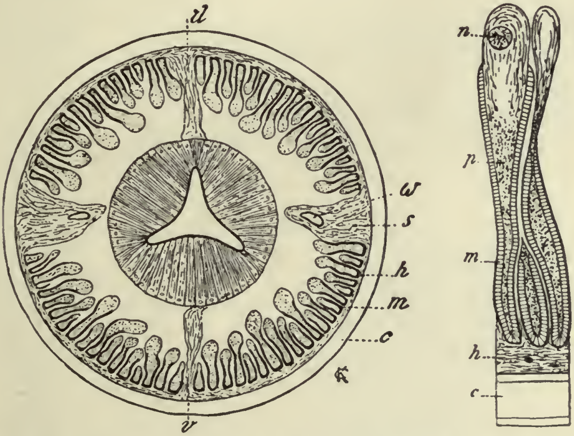


FIG. 259.—Section of *Ascaris lumbricoides* through the pharyngeal bulb; beside it a bit of the body wall more enlarged. *c*, cuticle; *d*, dorsal line; *h*, hypodermis; *m*, longitudinal muscle; *n*, nucleus of muscle cell; *p*, muscle cell; *s*, lateral line; *v*, ventral line; *w*, excretory canal.

specialized parts of the cœlomic epithelium and their products are usually carried to the exterior by the nephridia (more rarely by special ducts), so that here, as in vertebrates, we can speak of a urogenital system. A closed blood system is now present, now absent. Little in general can be said of the nervous system; details will be given in connexion with the separate classes.

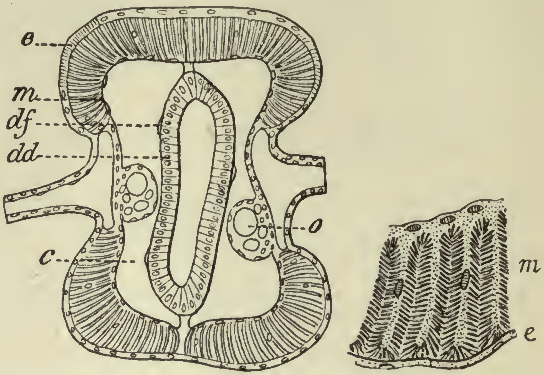


FIG. 260.—Transverse section of *Sagitta bipunctata* and a bit of the body wall more enlarged. (After O. Hertwig.) *c*, cœlom; *dd*, entoderm; *df*, splanchnic mesothelium; *e*, epidermis; *m*, somatic mesoderm (muscles and epithelium); o, ovary.

Class I. Chætognathi.

These marine forms, a half to two inches long, perfectly transparent, are well adapted to serve as an introduction to the cœlomate worms. They live at the surface of the sea, preying on other animals, and from their shapes and rapid motions deserve the name *Sagitta*—arrow—given some forms. The animals swim by means of horizontal fins, one surrounding the tail and one or two pairs on the sides of the trunk (fig. 261). On either side of the mouth is a lobe bearing strong bristles used in seizing prey (Chætognathi, bristle-jaw). Internally the body is divided into three segments, head, trunk, and tail, by transverse septa which divide the cœlom into corresponding parts. Each segment of the cœlom again is divided into right and left halves by a mesentery (fig. 260), supporting the straight intestine, running lengthwise through it. The intestine terminates at the anus at the end of the trunk segment.

The nervous system is entirely ectodermal. In the head is a pair of fused cerebral ganglia (fig. 262), in the trunk segment a large ventral ganglion, and these are connected by long œsophageal commissures. Of interest, because characteristic of nematodes and many annelids, are the relations of the musculature, which consists of longitudinal fibres alone. The body cavity is lined with epithelium (fig. 260), which, so far as it abuts against the alimentary tract, is called splanchnic (or visceral) mesoderm; that on the side of the cœlom towards the ectoderm is the somatic mesoderm. The muscles arise from the latter layer and are divided into four fields, right and left dorsal, right and left ventral. The sex cells also arise from the epithelium of the cœlom, the eggs in the trunk segment, the sperm in the tail. The eggs are carried to the exterior by special ducts. The sperm-forming cells early lose their connexion with the epithelium, fall into the cœlom, where they develop the spermatozoa. These are carried out by canals which by their relations to the cœlom recall the nephridia of the annelids.

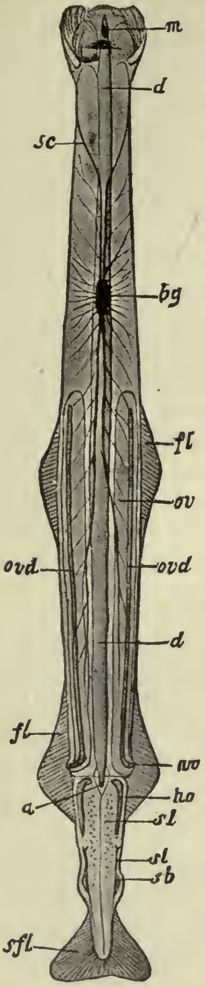


Fig. 261.

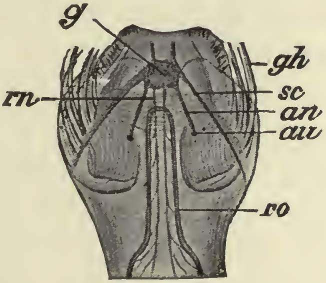


Fig. 262.

Fig. 261.—*Sagitta hexaptera*, ventral view. (After O. Hertwig.) *a*, anus; *bg*, ventral ganglion; *d*, intestine; *fl*, fin; *ho*, testes; *m*, mouth; *ov*, ovary; *ovd*, oviduct; *sb*, seminal vesicle; *sc*, œsophageal commissure; *sfl*, tail fin; *sl*, sperm; *wo*, female opening.

Fig. 262.—Head of *Sagitta bipunctata*, dorsal view. (After O. Hertwig.) *an*, nerve to *au*, eye; *g*, brain; *gh*, bristles; *rn*, nerves to *ro*, olfactory organs; *sc*, œsophageal commissure.

The development of *Sagitta* is significant from two points of view. The archenteron (fig. 108) is divided by lateral folds into an unpaired middle portion and two paired lateral chambers; the first is the definitive digestive tract, the latter the anlagen of the cœlomic diverticula.

In other words the cœlom is an outgrowth from the archenteron, *i.e.* is an enterocœle. Second: The gonads are derived from a pair of cells in the primitive entoderm, which later are carried into the cœlomic walls. Hence each divides into anterior and posterior cells, the anterior developing into the ovary, the posterior into testes. Hence here the male and female sex cells are beyond doubt descendants of a common mother cell.

The few species of Chætognathi are arranged in two or three genera, of which *Sagitta*, represented on our coasts by *S. elegans*,* is best known. *Spadella.*

Class II. Nemathelminthes.

Like the flatworms, the roundworms are characterized by their shape, they being thread-like or cylindrical animals whose form is the result of the existence of a body cavity in which the viscera are so loosely held that on cutting through the muscular body wall they will fall out (fig. 259). Since the Nemathelminthes share this cœlom with most annelids, the distinction between the two rests largely upon negative characters, the roundworms lacking the segmentation of the body cavity and the corresponding ringing or annulation of the body wall. To the Nemathelminthes belong three orders, much alike in habits and appearance but differing considerably in structure. Of these the most important are the nematodes.

Order I. Nematoda.

The nematoda contain numerous species of thread-shaped worms varying from 0.001 to 1.0 metre in length, many of which, through their wide distribution as parasites in plants, animals, and man, possess special interest. The outer surface is covered by a tough cuticle secreted by the underlying hypodermis (fig. 259), a layer corresponding to epithelium and cutis, which in cross-section shows, median and lateral, four thickenings, the dorsal, ventral, and lateral lines. In the lateral lines run the excretory vessels, two longitudinal canals which are united near the head by a transverse vessel opening on the ventral surface by an unpaired porus excretorius to the exterior. They are related to the cœlom by two giant cells on either side which send processes into the body cavity. These lateral and median lines divide the muscles (here only longitudinal) into four fields, as in Chætognaths. These muscles are parts of the somatic epithelium, a layer of vesicular cells which by their size (fig. 259) so encroach upon the cœlom that scarce space is left for the alimentary canal and reproductive organs. A splanchnic mesoderm is lacking.

The alimentary canal begins with a terminal mouth and ends with the anus, which is ventral and in front of the end of the body.

The mouth connects with the muscular œsophagus, which, for sucking purposes, is expanded posteriorly to a pharyngeal bulb and is lined throughout with a cuticle. From this point to the anus the stomach-intestine is usually uniform (fig. 263). The œsophagus is surrounded by a nervous ring which sends forward and back a large number of nerves, those in the mid-dorsal and ventral lines being strongest. At points on these nerves are collections of ganglion cells, but a formation of ganglia, as in the annelids, does not occur (fig. 264).

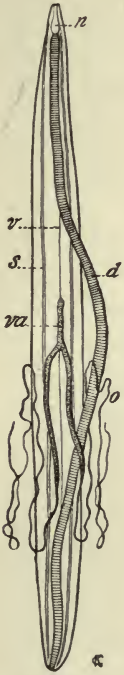


Fig. 263.

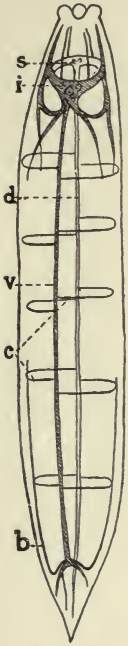


Fig. 264.

Fig. 263.—Structure of young female *Ascaris* (based on a drawing by Leuckart). *d*, intestine; *o*, ovary; *s*, lateral line; *v*, ventral line; *va*, vagina.

Fig. 264.—Diagram of nervous system of a nematode. (After Bütschli.) *c*, commissures; *d*, dorsal nerve; *i*, infraœsophageal, *s*, supraœsophageal part of nerve ring; *v*, ventral nerve.

The sexual organs of these rarely hermaphroditic forms are very simple. Males and females are easily distinguished not only by the copulatory organs, but by the openings of the genital ducts. These, in the male (fig. 265), are in the end of the alimentary canal, which hence is a cloaca. In the female (fig. 263) there is a special genital opening on the ventral surface between mouth and anus, the position varying with the species. In general the structure of the reproductive organs is alike in both sexes. In both, on account of the great fertility, these are long tubes coiled forward and back and ending in fine threads which produce eggs or sperm (ovaries, testes), while the rest serves as seminal vesicle, or receptaculum seminis, and ducts. In the male the genital tube is always single; in the female it is usually double, the right and left halves uniting a little before the external opening (fig. 263, *va*). Most common of copulatory organs in the male are spicula, bent spines, which lie in a sheath behind the vent and can be protruded through the cloacal opening, appropriate muscles causing them to retract. Besides there may be valves to right and left to clasp the male, or, as in *Trichina,* the whole cloaca is protrusible.

Since there is copulation, the eggs are fertilized in the uterus, after which they are either laid or retained for more or less of their development, many, like *Trichina,* being viviparous. The post-embryonic development depends largely upon the mode of life. Free-living species grow by repeated molts without much change of form. In many Anguillulidæ, which show how free life can be transformed into parasitic, there is an alternation of generations (heterogony) from an hermaphroditic entoparasitic to a free diœcious generation. The occasional suppression of the free generation which occurs in many Anguillulids leads to the Strongylidæ, where the offspring of the parasitic generation can live free for a time (rhabditis larvæ), but must return to parasitism to undergo a metamorphosis and become sexually mature. The free life is shortened again in the Ascaridæ, where the eggs must pass to the exterior for a longer or shorter time, but the embryos only escape when the eggs are taken into another host. Lastly, there are species like *Trichina* where the free life is entirely suppressed and transportation from host to host takes place in the encysted condition passively by food.

Family 1. ANGUILLULIDÆ; small thread-like nematodes with double pharyngeal swelling which live in mud, organic fluids or plants, rarely in animals; male with two spicula. *Anguillula aceti*, vinegar eel, 2 mm. long, in vinegar and stale paste. *Rhabditis* (*Rhabdonema*) *nigrovenosa*, not 1 mm. long, lives in mud and stands in heterogony with a second form which lives in the lung of frogs. *Strongyloides intestinalis* of the tropics, but which has recently appeared in southern Europe, has a somewhat similar history, the adult stage being reached in the human intestine. Here also belong numerous plant parasites of which *Tylenchus tritici* and *Heterodera schachti* demand notice, the first doing great damage to wheat, the second to turnips in Europe. *Tylenchus devastatrix* attacks rye and hyacinths.

Family 2. ASCARIDÆ. Mouth surrounded by three lips, one dorsal, two ventral; males with two spicules. Besides numerous species in lower vertebrates two of the most common parasites of man, the human roundworm and the pinworm, belong here. The former, *Ascaris lumbricoides*,* inhabits the small intestine, often in enormous numbers. The females average about 5–6 inches, the males 4 inches, in length. The animals are enormously prolific, a female containing about 60,000,000 eggs. The eggs (fig. 246, *a*) are easily recognized. Shortly after fertilization the eggs pass out of the intestine with the fæces, but develop without intermediate host if in the course of two or three months, when the embryo has developed, they are taken into the human intestine. The development of the pinworm, *Oxyuris vermicularis*,* is somewhat similar except that the embryos are developed in the egg at the time of oviposition, and hence after a shorter stay outside the body are capable of infection. The white worm, not half an inch long, lives in the rectum, especially of children, and in crawling outside the anus causes intolerable itching. *Ascaris mystax** occurs in dogs and cats (occasionally in man). *A. megalocephala** (a favorite animal for cytological researches) and *Oxyuris equi* in the horse. These do little harm. On the other hand *Heterakis maculosa* often destroys whole flocks of pigeons.

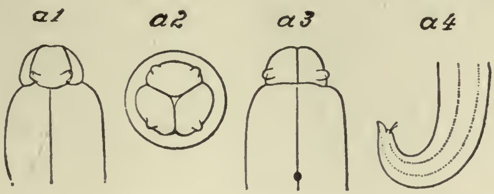


FIG. 265.—Dorsal, end, and ventral views of head and hinder end of male *Ascaris lumbricoides.* (From Hatschek.)

Family 3. STRONGYLIDÆ. These are readily recognized by the bursa of the male, a broadening of the hinder end of the body by two ring-like processes, which contains two spicula. Frequent but not constant is a widened capsule surrounded by papillæ at the mouth. A number of species of *Strongylus* occur in domestic animals. *Syngamus trachea-*

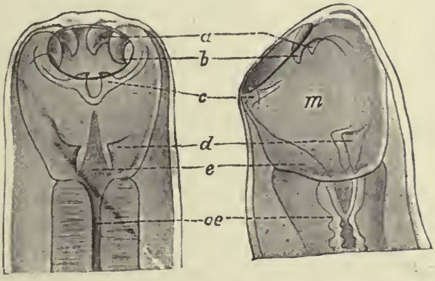


FIG. 266.—Anterior end of *Ankylostomum duodenale*, dorsal and side views. *a*, inner, *b*, outer ventral teeth; *c*, dorsal tooth of *m*, mouth capsule; *d*, stylet; *e*, ventral ridge; *oe*, œsophagus.

lis,* half to three quarters of an inch in length, the male and female always in pairs, cause the disease known as 'gapes' in fowl. *Ankylostomum* (*Dochmius*) *duodenale**(fig. 266), about two fifths of an inch in length, lives in the small intestine of man, causing severe loss of blood and the disease known as Egyptian chlorosis. The eggs develop in mud and moist earth, and hence people who drink muddy water (Fellahin of Egypt) or work much with clay (potters and brick-makers) are especially subject to infection. It was first known in Egypt, caused considerable trouble during the building of the St. Gotthard tunnel in Switzerland, and now is common in Germany. Recently it has been thought that the *Ankylostoma* larvæ obtain entrance to man through the skin, as in bathing, etc.

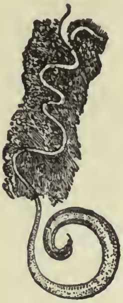
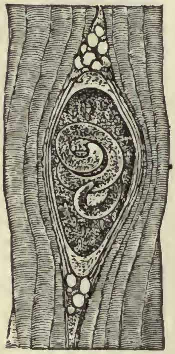


FIG. 267.



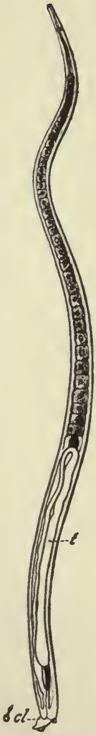


FIG. 269. FIG. 268.

FIG. 267.—*Trichocephalus dispar*, male with anterior end imbedded in intestinal wall. (From Leuckart.)
FIG. 268. — *Trichina spiralis*, male. (From Hatschek). *cl*, cloaca; *t*, testes.
FIG. 269.—*Trichina* in muscle. (From Boas.)

Family 4. TRICHOTRACHELIDÆ. These owe their common name of 'hair necks' to the fact that the part of the body which contains the pharynx is hair-like and elongate, while the pharynx itself traverses a peculiar cord of cells. Longest known of the family is *Trichocephalus dispar* * of man (fig. 267), about an inch or an inch and a half in length, which lives with its neck burrowed like a corkscrew in the wall of the intestine near the cæcum. Since it does not move, it causes little injury. Its presence can be recognized by the oval brown double-shelled eggs (fig. 246, *d*) in the fæces.

A second species, *Trichina spiralis* * (figs. 268, 269), is much smaller, but much more dangerous. Two stages are to be distinguished, the encysted muscle *Trichina* and the sexually mature intestinal *Trichina*. The first was discovered in a human body in 1835; the latter was not known until much later, its history being worked out by Leuckart, Virchow, and Zenker. In the encysted stage it occurs in the muscles of pigs, rats, mice, man, rabbits, guinea pigs, dogs, etc. (never in birds), enclosed in an oval capsule about 0.4 to 0.6 mm. long and hence recognizable by a practised observer with the naked eye. They are more easily seen when they are partially calcified and have a whitish color. Certainty in their recognition demands a low power of the microscope. In the capsule is coiled up the worm, about 1 mm. long, which is not yet sexually mature, although furnished with the anlagen of sexual organs. To attain this it must be transported into the intestine of another host. When, for instance, man eats trichinosed pork the worms are freed from the muscle and capsules by the digestive fluids and, entering the small intestine, become sexually mature in a few days. The female (3–4 mm. long, the male 1.5 mm.) penetrates into the superficial layer of the intestinal villi and in course of a month gives birth to 1500 (some say 10,000) living young, after which she dies. The young, on the other hand, penetrate the lymph vessels, and by way of the thoracic duct are carried into the blood-vessels, and wander from the capillaries into the muscles, especially those which are much worked, like the diaphragm, eye muscles, and muscles of the neck, and which consequently have a rich blood supply. They enter the sarcolemma of the muscle, destroy the muscle substance, and finally become enclosed by a capsule secreted by the host. The wandering takes place about the second or third week after infection, the encystment in about three months. A slight infection causes disagreeable symptoms; but where large numbers obtain entrance the cases are frequently fatal. The worst epidemic known was in Emmersleben, Saxony, in 1884, where 57 died in four weeks from infection from one pig.

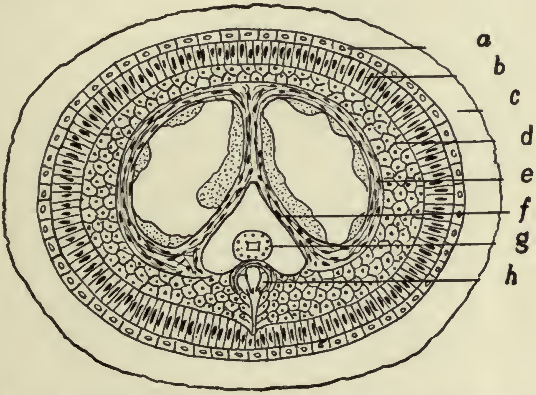


FIG. 270.—Transverse section of young *Gordius*. (After von Linstow.) *a*, hypodermis; *b*, muscular layer; *c*, cuticle; *d*, parenchyma; *e*, *f*, muscles and mesenteries; *g*, alimentary canal; *h*, nervous system.

Family 5. FILARIIDÆ. These are extremely elongate, hair-like worms. Their best-known representative is *Dracunculus medinensis*, the guinea worm (the female about a yard long, and about as large as stout packing twine), which produces a sickness known to the Greeks as dracontiasis. It forms abscesses beneath the skin in which the worm is coiled up. The embryos break through the wall of the mother and must enter the water and penetrate a small crustacean, *Cyclops*. It is apparently introduced into the human system by swallowing the crustacea with drinking water. The worm has recently been found in the tropics of America.

A second species is *Filaria sanguinis hominis*, the adults of which—3 to 6 inches long—live in the lymphatic glands of man, while the young escape into the blood, often in immense numbers. They often escape through the kidneys, where they produce serious disturbance (albuminuria, hæmaturia). There is possibly a connexion between them and elephantiasis. The intermediate host is apparently the mosquito. As yet they are known only in the tropics. Other species occur in man and other animals.

Family 6. MERMITHIDÆ. Elongate nematodes with six oral papillæ. They live in the body cavity of insects and pass into damp earth, where they become sexually mature. They share with the Gordiacea the common name 'hairworms.' *Mermis.**

Order II. Gordiacea.

The hairworms resemble the nematodes in general appearance, but differ greatly in structure. The body cavity has both splanchnic and somatic epithelium; the intestine is supported by mesenteries; there is an œsophageal nerve ring and unpaired ventral nerve cord, and the female genitalia enter the cloaca. The adults live in water, where they lay their eggs; the larvæ live in insects, there being in some cases at least an alternation of hosts. These (and the Mermithidæ) are popularly believed to be horse hairs changed into worms. *Gordius*,* *Chordodes.**

Near the Gordiacea must be mentioned the marine *Nectonema*,* the young stages of which are apparently passed in the mosquito.

Order III. Acanthocephala.

The species of spine-headed worms live in the alimentary canal of vertebrates. In appearance they resemble the Ascaridæ (p. 301), but are easily distinguished by the proboscis, which may be retracted by muscles and exserted by contraction of the muscular body wall. This proboscis bores into the intestinal wall and is held in place by numerous retrorse hooks (fig. 271). In internal anatomy the entire absence of an alimentary canal marks them off from Nematodes and Gordiacea, as also the peculiar structure of the reproductive organs and a closed vascular system in the body wall which extends into two sacs, the lemnisci, lying beside the proboscis sheath. The unpaired ganglion lies on the proboscis sheath between the lemnisci. An intermediate host occurs in development, the larva living in an arthropod. Thus the larva of *Echinorhynchus* (*Gigantorhychus*) *gigas** of the pig lives in the larva of the 'June bug' (*Melolontha*), that of *E. proteus* of European fresh-water fishes in crustacea. One species, *E. hominis*, is extremely rare in man.

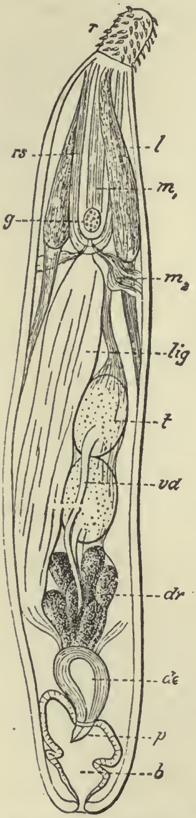


FIG. 271.—Male *Echinorhynchus angustatus.* (From Hatschek.) *b*, penis sac; *de*, seminal vesicle; *dr*, glands; *g*, ganglion; *l*, lemnisci; *lig*, ligament; $m_1 m_2$, retractors of proboscis and its sheath; *p*, penis; *r*, proboscis; *rs*, proboscis sheath; *t*, testes; *vd*, vas deferens.

Class III. Annelida.

The segmentation of the body, which was shown in a slight degree in the Chætognathi, reaches its highest development in the Annelids, where it appears both in the outer ringing of the body and in the arrangement of the most important systems of organs—metameric arrangement of excretory organs, nervous system, blood-vessels—internal segmentation. To this is added an extraordinary increase in number of body segments (somites, metameres), which can far exceed a hundred. We can thus define the Annelids as

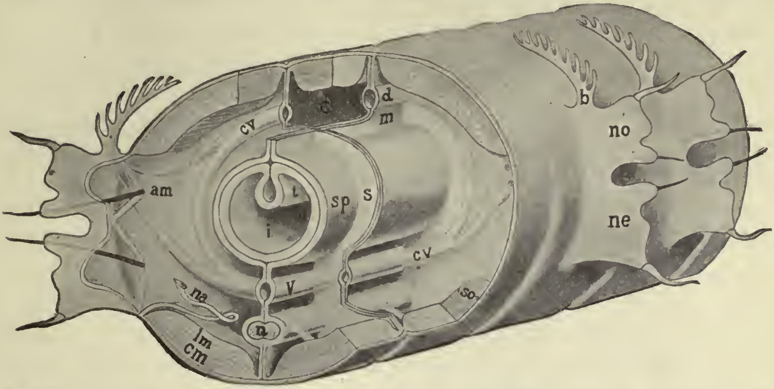


FIG. 272.—Diagram of annelid somites (orig.). *am*, acicular muscles; *c*, cœlom; *cm*, circular muscles; *cv*, circular blood-vessels; *d*, dorsal blood-vessel; *i*, intestine; *lm*, longitudinal muscles; *m*, mesentery; *n*, nerve cord; *na*, nephridium; *ne*, *nv*, neuro- and notopodia, forming parapodium; *s*, septum; *so*, somatopleure; *sp*, splanchnopleure; *t*, typhlosole.

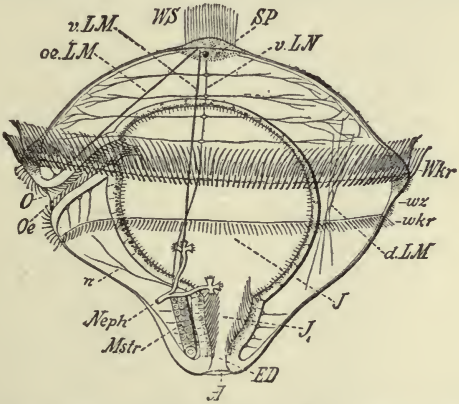


FIG. 273.—Trochophore (Loven's larva) of *Polygordius.* (From Hatschek.) *A*, anus; *dLM*, dorsal muscles; *ED*, hind gut: *J*, stomach; J_1, intestine; *Mstr*, mesodermal band; *n*, nerves; *Neph*, protonephridia; *O*, mouth; *Oe*, œsophagus; *oeLM*, œsophageal muscle; *SP*, apical plate; *vLM*, ventral muscle; *vLN*, lateral nerve; *Wkr*, *wkr*, pre- and post-oral zones of cilia; *WS*, apical cilia; *wz*, adoral cilia.

worms with cœlom and with external and internal segmentation. In the development there frequently occurs a type of larva, the trochophore, which must be referred to here, since it is of great morphological significance, resembling in structure the rotifers and recalling the larva of the molluscs and to a less extent that of the echinoderms. It is (fig. 273) a gelatinous body traversed by an alimentary canal with fore-, mid-, and hind-gut regions. At first it is everywhere ciliated, but with advance of development the cilia become restricted to certain thickened tracts of epithelium, the ciliated bands. One of these, the preoral band, is especially constant. It runs circularly (*Wkr*) around the body, surrounding a circular prestomial area, in the centre of which is the anlage of the cerebral ganglia, a thickened patch (apical plate) of ectoderm, often bearing a tuft of cilia. Other ciliated bands (post-oral, perianal) often occur. Of internal organs, besides numerous muscle fibres, the most noticeable are the excretory organs, true protonephridia, which open to the exterior either side below. The trochophore in some respects resembles the larvæ of some Turbellaria (fig. 231) and Nemertines (fig. 256), showing that the annelids are related to these groups.

The above account applies most closely to the Chætopoda and the closely related Archianellida. In other forms one or more features may be lacking—in the Gephyræa segmentation of the body; in the Hirudinei most of the cœlom and the trochophore. Yet these are so closely related that they must be included under the common head; the missing characters have been lost during evolution.

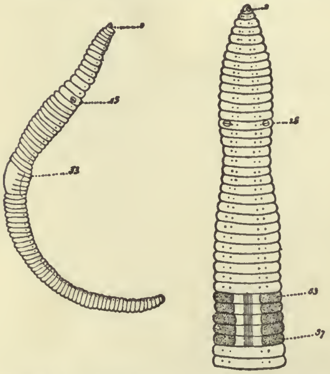


Fig. 274.—Earthworm, side view and anterior end enlarged. (After Vogt and Jung.) 1, first segment with mouth and prostomium; 15, male sexual opening; 33–37, clitellum.

Sub Class I. Chætopoda.

These, like the Nematoda, are cylindrical worms, but are at once distinguished by the segmentation. Deep circular constrictions (fig. 274) bound the somites externally. Internally the cœlom is divided by the septa—delicate double membranes which extend from the ectoderm to the alimentary canal—into as many chambers as there are metameres, while a longitudinal mesentery, also double, separates the cœlomic pouches of the right side from those of the left (figs. 275 and 272). The alimentary canal also shows distinctions; for while it differs greatly in the various species, it has constantly a terminal anus, while the mouth is ventral and is overhung by the preoral segment, the prostomium.

Nervous system, blood-vessels, and excretory organs are influenced by the segmentation. The nervous system is built on the ladder plan. It begins with a supraœsophageal ganglion ('brain') lying in the prostomium, from which the œsophageal commissures pass around the œsophagus to form the ventral chain, which consists of as many pairs of ganglia, united by longitudinal commissures, as there are somites present. These ganglia of the ventral chain are closely similar, since the segmentation of the body is homonymous. There is but the slightest division of labor among the somites, and hence they differ but slightly among themselves. The prostomium always bears tactile organs and frequently eyes, which in many marine forms are highly developed, with lens, vitreous body, and retina. Otocysts are rare, but occur in diverse species. Ciliated pits (olfactory) occur on the head, goblet organs (taste) on head and trunk, and, lastly, lateral organs, sensory structures of unknown function, may be metamerically arranged.

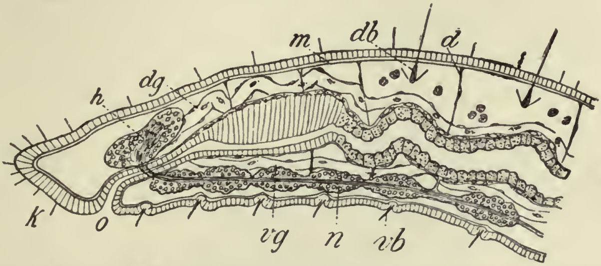


Fig. 275.—Anterior end of *Nais elinguis*. *h*, cerebrum, connected by commissure with ventral chain, *n*; *dg*, contractile dorsal, *vg*, ventral blood-vessel; *m*, muscular layer of skin; *db*, *vb*, dorsal and ventral chætæ; *d*, septa; *k*, prostomium; *o*, mouth.

The blood-vessels are most frequently represented by two main trunks which frequently (as in earthworms) contain blood colored red by hæmoglobin. One trunk runs dorsal, the other ventral, to the intestine, the two being connected by vessels (figs. 272, 276) in each segment. The blood passes forward in the dorsal vessel, backwards in the ventral. It is propelled by contractile portions of the vessels; usually the dorsal vessel pulsates, but, as in the earthworms, certain of the circular vessels in the anterior part of the body may function as hearts (fig. 276, *c*). Rarely, as in the Capitellidæ, circulatory organs may be lacking.

The excretory organs (nephridia) were formerly known as 'segmental organs,' since they occur in pairs in each segment. These supplant the embryonic protonephridia; each consists of an internal ciliated funnel, the nephrostome, a more or less convoluted tube, and the external opening (fig. 69). In many instances (Oligochætes, some Polychætes) the nephrostome is in one somite, the external opening in the succeeding. The nephridia also usually serve as genital ducts, carrying away the reproductive cells, which

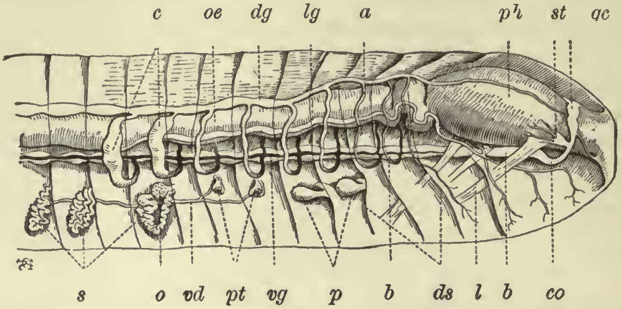


FIG. 276.—Anterior end of *Pontodrilus marionis*. (After Perrier.) *a*, vascular arches; *b*, ventral nerve chain; *c*, 'hearts'; *co*, œsophageal commissure; *dg*, dorsal blood-vessel; *ds*, septa; *gc*, cerebrum; *l*, retractors of pharynx; *lg*, lateral blood-vessel; *o*, ovary; *oe*, œsophagus; *p*, receptacula seminis; *ph*, pharynx; *pt*, ciliated funnels of vas deferens; *s*, nephridia; *vd*, vas deferens.

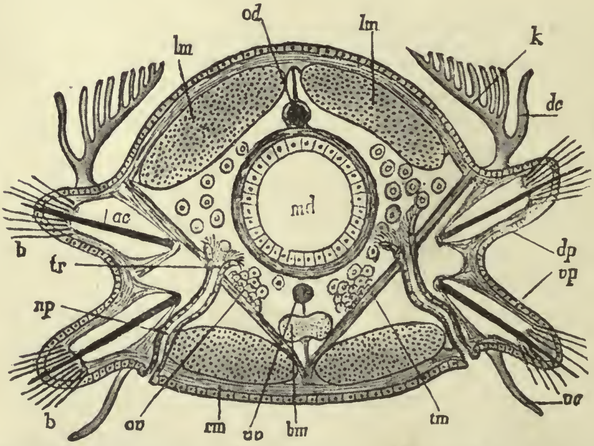


FIG. 277.—Schematic cross-section of an annelid. (After Lang.) *ac*, aciculum; *b*, chætæ; *bm*, ventral nerve cord; *dc*, dorsal cirrus; *dp*, notopodium; *k*, gill; *lm*, longitudinal muscles; *md*, digestive tract; *np*, nephridium; *ov*, ovary; *rm*, circular muscles; *tm*, transverse muscles; *tr*, nephrostome; *vc*, ventral cirrus; *vd*, *vv*, dorsal and ventral blood-vessels; *vp*, neuropodium.

always arise from the cœlomic epithelium. In the Oligochæta (fig. 286), besides the nephridia in the genital segments special oviducts and vasa deferentia occur which are usually regarded as modified nephridia.

Of the many modifications of nephridia only a few can be noticed here. Occasionally there may be more than one pair in a somite, or they may have more than one nephrostome. Again, they may be lacking from more or fewer somites. In many Oligochætes they may empty into the anterior or posterior ends of the digestive tract. In many (*Glycera*, *Hesione*, *Nephthys*, *Goniada*) the internal ends of the nephridia are branched, the branches being closed by ‘solenocytes,’ tubular cells bearing an internal bundle of cilia.

In many marine annelids there occurs a metamorphosis in which pelagic larvæ occur. These, in spite of their many modifications, are comparable with the ‘Loven's larva,’ the trochophore already described (p. 306). The differences largely consist of modifications of the ciliary apparatus; the number of bands may be increased (polytroche larvæ), or a single band may occur at the middle (mesotroche) or at the end (telotroche) of the body. The larva becomes a segmented worm by the hinder end of the larva growing out and dividing into segments (fig. 278). In this

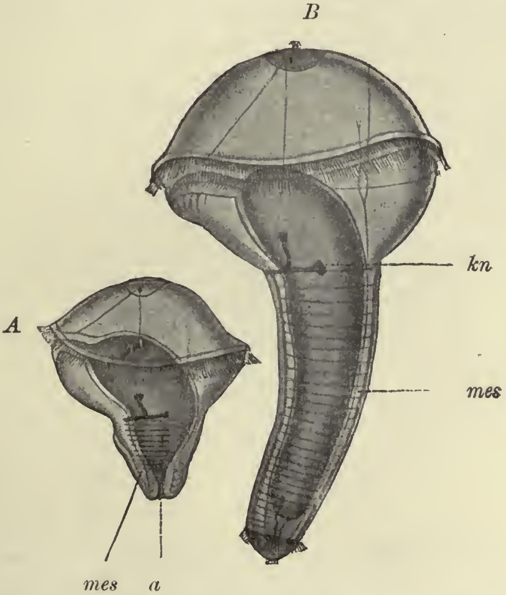


FIG. 278.—*A*, larva of *Polygordius*; *B*, same changing to segmented worm. (After Hatschek.) *a*, anus; *kn*, excretory organ; *mes*, segmented mesoderm.

jointed portion the cœlom arises as a new formation, divided from the first into separate chambers. The nephridia also arise *de novo,* independent of the protonephridial system, which is often called head kidney because the chief part of the trochophore forms the head of the adult.

The fresh-water annelids develop directly, but the embryos possess a reminiscence of an earlier larval life in that the head lobes are very apparent and contain protonephridia, which leads to the conclusion that these animals earlier had a metamorphosis. From the resemblance of the trochophore to the Rotifera the farther conclusion is drawn that the annelids have descended from Rotifer-like ancestors, the body cavity, nephridia, blood-vessels, and ventral nerve chain being new formations.

Besides sexual reproduction many fresh-water and marine species may reproduce asexually, this being rendered possible by the great homonymy of the segmentation. By rapid growth at the hinder end as well as at a more anterior budding zone numerous somites are formed which separate in groups from the parent to form young worms. In some cases the formation of new somites may take place more rapidly than the separation, the result being chains of worms (fig. 279).

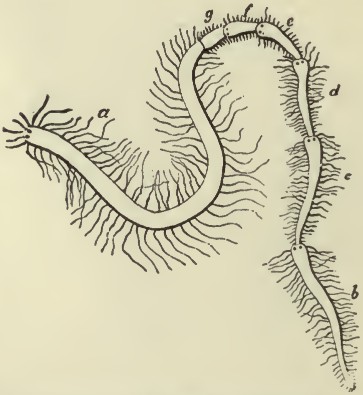


Fig. 279.—Budding in *Myrianida.* (After Milne-Edwards.) The sequence of letters shows the ages of the individuals.

By a combination of sexual and asexual reproduction a typical alternation of generations occurs, the origin of which receives light from the following facts: In many polychætes which reproduce exclusively by the sexual process the sexless slowly-moving young (atoke) at sexual maturity becomes so altered in appearance as to have been described under another name. It becomes very active in its movements, and the hinder somites, which contain the sexual organs, develop special bristles and parapodia (fig. 284, *A*). Thus many species of *Nereis* pass into the '*Heteronereis*' stage. In other Polychætes the sexual part (epitoke) separates from the sexless atoke portion and swims freely, while the atoke produces new epitokes. In the Samoan Islands *Eunice viridis* reproduces in this way, the epitokes coming to the surface at certain times in incredible numbers, forming the 'palolo worm,' a delicacy in the Samoan diet. In still other species the epitoke regenerates the head and thus becomes an independent generation. *Syllis* and *Heterosyllis* are thus related. The Autolytidæ furnish the most complication. Here the atoke, by budding as in *Myrianida*, fig. 279) forms chains of dimorphic individuals which later separate. The individuals of male chains were formerly described as '*Polybostrichus*,' the females as '*Sacconereis*.' This same homonymy explains the regenerative powers of many worms. Thus if certain earthworms be cut in two, they will continue to live and will reproduce the lost parts.

Another important character of the Chætopoda is the possession of bristles or chætæ. These arise in special follicles, singly or several in a bunch, of which usually there are four—right and left, dorsal or lateral and ventral—in each somite. Each follicle (fig. 280) is a sac of epithelium opening on the surface and having at the base a special cell for the development of each bristle. The developed bristles project from the follicle and, moved by appropriate muscles, form small levers of use in locomotion. Their numbers, shape, and support are of much systematic importance.

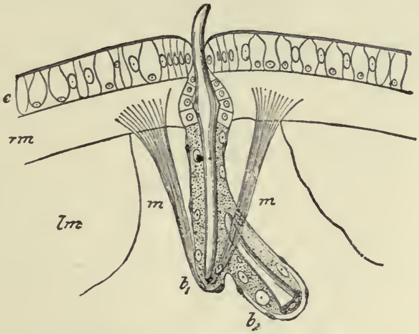


FIG. 280.—Arrangement of a bristle in an Oligochæte. (After Vejdowski.) *e*, epithelium; *rm*, *lm*, circular and longitudinal muscles; *m*, muscle of the follicle; b_1, chæta follicle, its chæta in function; b_2, follicle for replacement, the formative cell at its base.

Order I. Polychætæ.

The Polychætæ owe their name to the fact that each group of bristles contains many chætæ; but more important is that the bristles of each side are supported by a fleshy outgrowth of the somite, the parapodium, in which two portions corresponding to the bunches of bristles—dorsal, notopodium; ventral, neuropodium—may be recognized (fig. 281). This is the first appearance of true appendages, but they differ from those of Arthropoda in that they are not jointed to the body nor jointed in themselves. On the dorsal surface may occur diverse outgrowths, known, according to position or function, as cirri, elytra, gills, etc.; on the head, palpi and tentacles. The cirri are long processes on the parapodia, and like palpi are tactile (fig. 281). Elytra are thin lamellæ which cover the back like shingles and thus protect the body.

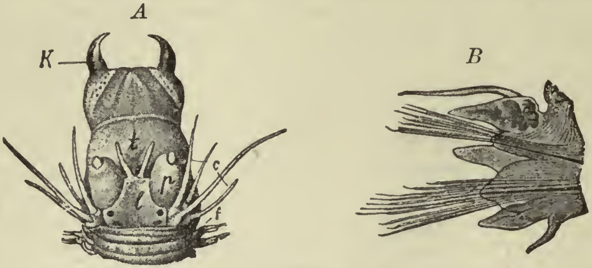


Fig. 281.—*A*, head with protruded pharynx; *B*, parapodium of *Nereis versipedata*. (After Ehlers.) *c*, cirri; *k*, jaws; *l*, head with eyes; *p*, palpi; *t*, tentacles.

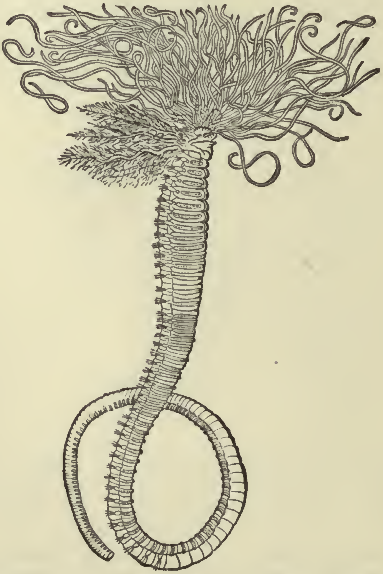


Fig. 282.—*Amphitrite ornata*.* (From Verrill.)

Nearly all Polychætes are diœcious and undergo a more or less pronounced metamorphosis; with few exceptions (*Manyunkia** from the Schuylkill, *Nereis** in California) they are marine. They are usually divided according to their habits into fixed (Sedentaria) and free forms (Errantia), but this classification lacks a morphological basis. The Sedentaria feed on vegetable matter, usually form tubes of leathery organic substances, in which foreign matter may be incorporated or which may be calcified. The worms project their anterior segments from the tubes. The Errantia often secrete gelatinous tubes in which they can hide, but they never lose their powers of locomotion, and from time to time leave their retreats and swim about preying on other animals. Correlated with habits are differences in structure. In the Errantia the head and trunk are not very different; the anterior part of the alimentary tract can be protruded as a proboscis, and, corresponding to their predaceous habits, is often armed with strong jaws (fig. 281, *A*). In the Sedentaria there are no such pharyngeal teeth, but, on the other hand, there is a greater difference between anterior and posterior somites. In the latter the parapodia are weakly developed, and this part resembles the Oligochætes in appearance. The head and beginning of the trunk (thorax) are richly provided with gills and tentacles for respiration and the taking of food (fig. 282).

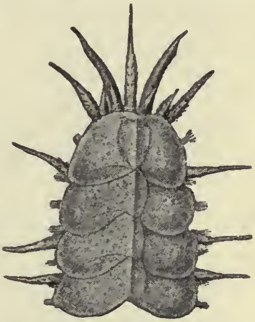


FIG. 283.—Head of *Polynoe spinifera.* (After Ehlers.) Back entirely covered with elytra; cirri and parapodia projecting at the sides.

Sub Order I. ERRANTIA. Predaceous annelids with strongly armed pharynx. The EUNICIDÆ, mostly represented on our shores by small species, contains some species a yard in length. *Diopatra*,* *Nothria.** The ALCIOPIDÆ are transparent pelagic forms with large, highly developed eyes. The SYLLIDÆ usually have three long tentacles; *Autolytus*,* *Myrianida** (p. 310). The POLYNOIDÆ* (*Lepidonotus*,* *Polynoe** (fig. 283), *Aphrodite aculeata*,* the sea mouse, 6 inches long) are bottom forms with elytra covering the back. NEREIDÆ; *Nereis virens*,* the clam worm of all northern seas.

Sub Order II. SEDENTARIA (Tubicola, Cryptocephala). These forms cannot wander about at will, but live in their tubes. In the SABELLIDÆ the tube is membranous and there is a crown of gills; *Myxicola*,* *Chone*,* *Manyunkia.** In the SERPULIDÆ the tube is calcified and is closed by an operculum on one of the gills. *Hydroides*;* *Spirorbis*,* forming coiled tubes on seaweed; *Protula.** The ARENICOLIDÆ,* which burrow in sand, have gills on the sides of the body. The MALDANIDÆ (*Clymene*,* *Axiothea**) have extremely long segments and build tubes of sand. The TEREBELLIDÆ (*Terebella*,* *Amphitrite* (fig. 282), *Thelepus**) have numerous filiform tentacles and branched gills on the anterior end.

The ARCHIANELLIDÆ, which lack bristles and parapodia, must be placed near the Polychætæ and are usually regarded as very primitive forms which in structure and development (fig. 273) are of importance in the phylogenesis of the Annelids. *Polygordius.**

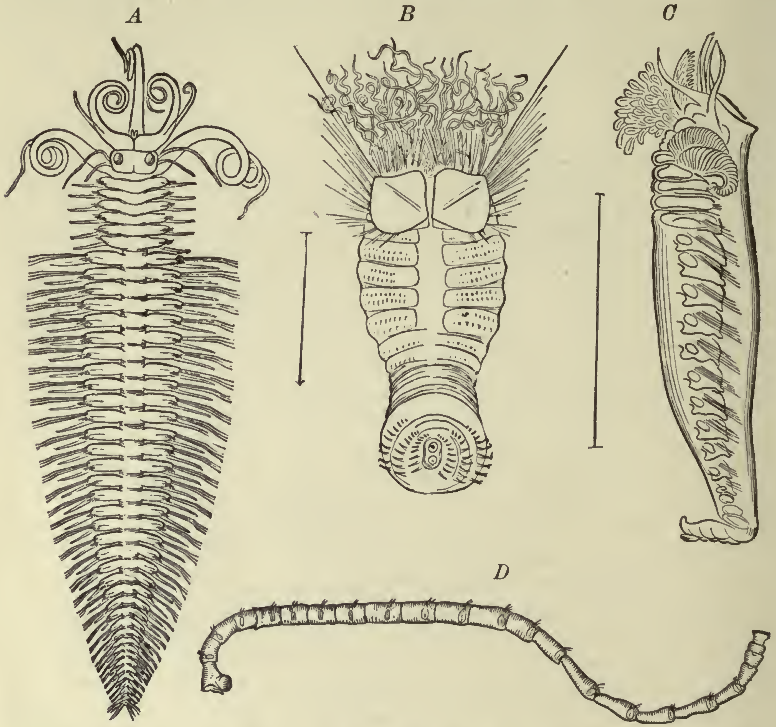


Fig. 284.—New England Annelids. *A*, male *Autolytus*; *B*, *Sternaspis fossor*; *C*, *Cistenides gouldii*; *D*, *Clymene torquata*. (From Emerton and Verrill.)

Order II. Oligochætæ.

The Oligochætes are almost as preeminently fresh-water and terrestrial forms as the Polychætes are marine. They are in most respects simpler than their marine relatives, apparently the result of degeneration, which has followed from the more simple conditions of existence. Eyes are rudimentary or lacking, they have no palpi, cirri, or tentacles; gills are rare, but most striking is the absence of parapodia, the bristles projecting directly from the body wall (fig. 280). The chætæ may be regularly distributed around each somite (*Perichæta*) or gathered on the sides (*Megascolex*) or arranged in four bunches so that in the animal four longitudinal rows occur. The animals are hermaphroditic, testes and ovaries lying in different somites. Usually the integument in the neighborhood of the sexual openings is thickened by the presence of numerous glands, forming a clitellum (fig. 274), which secretes the egg cocoons. The clitellum also functions in copulation, secreting bands which hold the animals together so that the sperm from one passes into the receptaculum seminis of the other. After impregation the eggs are usually enclosed in cocoons.

Sub Order I. LIMICOLA (Microdrili.) Mostly fresh-water forms. The TUBIFICIDÆ, in consequence of the red blood, when present in large numbers color the bottom red. They quickly retract into the tubes which they form in the mud. *Tubifex*,* *Petoscolex; Clitellio irroratus** common on our seashores. The NAIDIDÆ are transparent forms living on water plants which reproduce asexually throughout nearly the whole year.

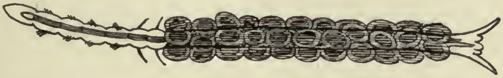


FIG. 285.—*Aulophorus vagus*, in tube of *Pectinatella* statoblasts. (After Leidy.)

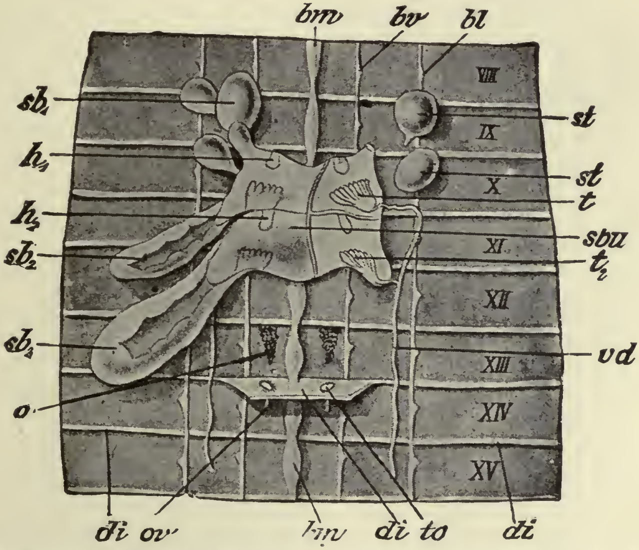


FIG. 286.—Sexual organs of *Lumbricus herculeus* (after Vogt et Jung): the seminal vesicles of the right side cut away. *bm*, ventral nerve cord; *bl*, *bv*, lateral and ventral rows of setæ; *di*, septa; h_1, h_2, testes, enclosed in sperm reservoir; *o*, ovaries; *ov*, oviducts; *sbu*, sperm reservoir; $sb_{1,\ 2,\ 3}$, sperm sacs (seminal vesicles): st_1, seminal receptacles; t_1, t_2, seminal funnels connected with the vasa deferentia; *to*, funnels of oviducts; *vd*, vas deferens.

*Dero** and *Aulophorus** have gills around the anus. ENCHYTRÆIDÆ; *Distichopus*, *Pachydrilus*. The DISCODRILIDÆ (*Bdellodrilus*, *Myzobdella*) are parasitic.

Sub Order II. TERRICOLA (Macrodrili). Here belong the terrestrial forms, the earthworms, our species of moderate size, in the tropics large species (*Megascolex australis* four feet long). Our species belong to *Lumbricus,** *Allobophora**; *Perichæta** has been introduced from the tropics; *Diplocardia** with double dorsal blood-vessel. Most species agree in habits; they burrow through the earth, swallowing the humus and casting the indigestible portions on the surface. They loosen the soil and are continually bringing the deeper parts to the surface, and thus do great good. Contrary to oft-repeated statements, earthworms occurred in our prairies and plains when first broken up by the plow. Details of the reproductive organs of one species are shown in fig. 286. These vary greatly and are largely used in classification.

Sub Class II. Gephyræa.

The exclusively marine Gephyræa are distinguished at the first glance from the Chætopoda by the entire absence of segmentation. The body is oval or spindle-shaped, circular in section. The mouth, at the extreme anterior end, is either surrounded by a circle of tentacles (fig. 287) and is retracted together with the anterior end of the body by internal retractor muscles, or is overhung by a

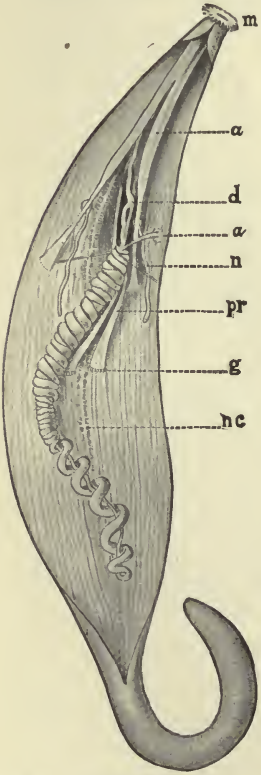


Fig. 287.

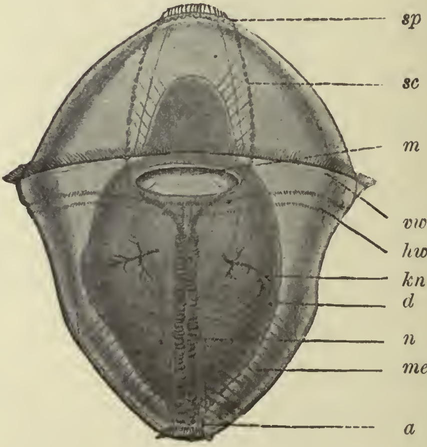


Fig. 288.

Fig. 287.—Anatomy of *Phascalosoma gouldi* (orig.). *a*, anus; *a*, anterior retractors; *d*, digestive tract; *g*, gonads; *m*, mouth; *n*, nephridia; *nc*, ventral nerve cord; *pr*, posterior retractors.

Fig. 288.—Larva (trochophore) of *Echiurus*. (After Hatschek.) *a*, anus; *d*, intestine; *hw*, postoral cilia; *kn*, protonephridia; *m*, mouth; *mes*, mesoderm bands with indication of segments; *n*, ventral nerve cord; *sc*, œsophageal commissure; *sp*, apical plate; *vw*, preoral ciliated band.

dorsal spatulate preoral lobe or 'proboscis' which may be several times the length of the body and forked at its tip (fig. 289).

Internal segmentation is also lost, septa being entirely lacking. The nephridia are also reduced in number, at most but three pairs being present, and in some but a single unpaired organ. They are sexual ducts, and in the Chætiferi there are special excretory organs (fig. 289, *g*) covered with branching canals opening to the body cavity by nephrostomes and emptying into the intestine. These resemble somewhat the branchial trees of the holothurians (*infra*), and hence these animals were formerly supposed to bridge the gap between holothurians and annelids, whence the name (*γέφυρα*, bridge) Gephyræa. The vascular and nervous systems are more like those of other annelids. The vascular system consists of a dorsal and usually a ventral longitudinal trunk; the nervous system of a brain, œsophageal collar, and ventral cord, the latter without division into ganglia. The relations of the Gephyræa to the Chætopoda are shown by the development. In some (Chætiferi) there is a trochophore (fig. 288) from which the worm arises, as in the Chætopoda, by growth at the hinder end; this at first has a segmented cœlom and nervous system, the metamerism being lost later.

Order I. Chætiferi (Armata, Echiuroidea).

With spatulate preoral lobe, often forked at the tip; at least a pair of ventral setæ; a trochophore in development. *Echiurus pallasii* * in our northern waters, *Thalassema* * farther south. In *Bonellia* there is a marked sexual dimorphism (fig. 289). The female is 2 to 3 inches long and has a proboscis 8 to 12 inches long. The male is only 1 mm. long, totally different in appearance, and lives parasitically in the œsophagus of the female (fig. 289, *B*).

Order II. Inermes (Achæta, Sipunculoidea).

Distinguished by lack of chætæ, the mouth surrounded by tentacles, and the dorsal and anterior position of the anus. The larva is a modified trochophore without preoral ciliated band and without segmentation; only two, sometimes but one, nephridia. *Phascalosoma* * common on our shores. *Phascolion strombi* * builds tubes in deserted snail shells. *Sipunculus.* *

Order III. Priapuloidea.

No tentacles, mouth with chitinous teeth, terminal anus, no nephridia; two protonephridia united with the sexual organs and opening either side of the vent. Development unknown. *Priapulus*, *Halicryptus*.

Sub Class III. Hirudinei (Discophori).

Three points of external structure clearly distinguish the leeches from the chætopods. First, the absence of bristles (except in *Acanthobdella*) and the presence of two suckers, one of which occurs on the posterior ventral surface and is used only for attachment and locomotion, the other, sometimes scarcely differentiated, surrounds the mouth and is used in sucking the food. In locomotion anterior and posterior suckers are alternately attached, the body being looped up and extended like that of a 'span worm.' The animals can also swim well by a snake-like motion of the whole body.

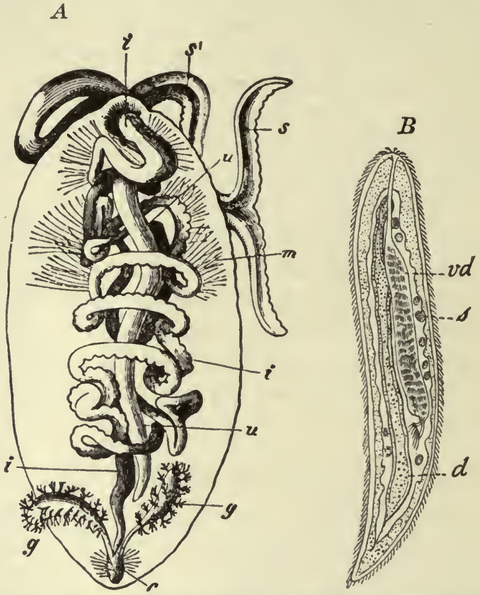


FIG. 289.—*Bonellia viridis.* *A*, female (after Huxley); *B*, male (after Spengel). *c*, cloaca; *d*, rudimentary intestine; *g*, excretory organ; *i*, intestine; *m*, muscles supporting intestine; *s*, balls of spermatozoa in *B*, in *A*, proboscis (preoral lobe); *u*, single segmental organ, functioning as oviduct; *vd*, nephridium with ciliated funnel serving as vas deferens.

A second point is the fine ringing of the body, there being usually many more rings than somites, the primitive segment rings being divided by secondary constructions, there being three, five, or even eleven rings to a segment. The middle or one of the anterior rings is often distinguished by bearing strongly developed sense organs. As in the earthworms, certain of the somites at the time of reproduction may develop into a clitellum which secretes the egg cocoons.

A third character is the marked flattening of the body in the dorsoventral direction (except in Ichthyobdellidæ and a few other forms), the animals thus recalling the flatworms. This may be the result of the very slight development of the cœlom. In most leeches there is a body parenchyma, traversed by longitudinal, transverse and dorsoventral muscles in which the organs are immediately imbedded (fig. 290).

The alimentary tract is provided with paired diverticula (fig. 291), varying in number in different species. Between the last and largest pair of these sacs is the intestine, which opens dorsal to the posterior sucker. The jawed and jawless leeches show considerable differences in the pharyngeal region. In the first there are three jaws in the phaynx, semicircular chitinous plates, the free edge of each armed with numerous calcified teeth (fig. 292). To these are attached two muscles, one to retract them, when not in use, into pockets, while the other exserts them and rotates them, causing a triradiate wound from which the blood flows. This bleeding is difficult to staunch, since glands on the lips and between the jaws produce a secretion which hinders the coagulation of the blood. In the jawless leeches a sharp conical process arising from the pharynx can be protruded from the mouth, and serves for wounding and sucking. The vascular system usually contains red blood, and consists, in the Gnathobdellidæ, of four longitudinal trunks, a dorsal, two lateral, and a

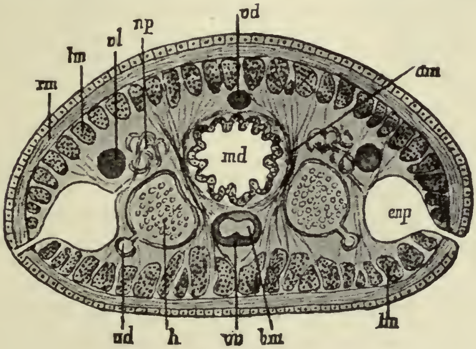


Fig. 290.

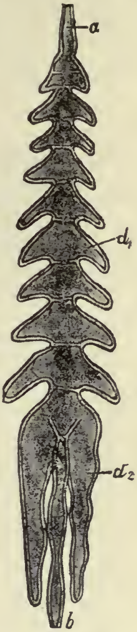


Fig. 291.

Fig. 290.—Transverse section of *Hirudo medicinalis.* (From Lang.) *dm*, *lm*, *rm*, dorsoventral, longitudinal, and circular muscles; *vl*, *vd*, *vv*, lateral, dorsal, and ventral blood-vessels, the latter surrounding the ventral nerve cord, *ni;* *h*, testes; *vd*, vas deferens; *md*, midgut; *np*, nephridial tubule; *enp*, urinary bladder.

Fig. 291.—Digestive tract of *Hirudo medicinalis.* (From Lang.) *a*, œsophagus; *b*, intestine; d_1, d_2, gastric diverticula.

ventral, the latter surrounding the ventral nerve cord. These are connected by a complicated system of capillaries.

The nervous system consists of brain and ventral cord, the latter containing frequently twenty-three ganglia (the first of five fused, the last of seven). Nerves from the brain go to the eyes. Right and left of the ventral cord are the hermaphroditic sexual organs. In *Hirudo medicinalis* (fig. 293) there are nine pairs of

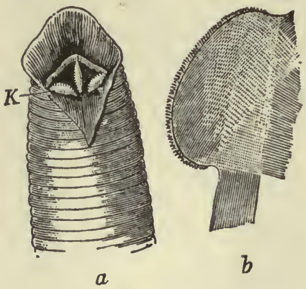


FIG. 292.

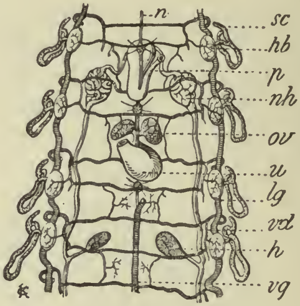


FIG 293.

FIG. 292.—*Hirudo medicinalis*, medicinal leech. (After Leuckart.) *a*, anterior end with three jaws (*k*); *b*, a single jaw with its muscles.

FIG. 293.—Nervous system, blood-vessels, sexual organs, and nephridia of a leech, ventral view. *h*, testes; *hb*, urinary bladder; *lg*, lateral blood-vessel; *n*, ventral nerve cord; *nh*, epididymis; *ov*, ovary; *p*, penis; *sc*, nephridia; *u*, uterus and vagina; *vd*, vas deferens; *vg*, ventral blood-vessel.

testes (*h*), the ducts of which unite to form a vas deferens on either side (*vd*). These pass forward, form by coiling a so-called epididymis (*nh*) and empty into the median unpaired penis (*p*). In the space between the epididymis and the first pair of testes are the ovaries (*ov*) and oviducts and an unpaired vagina (*u*). The nephridia (17 pairs in this species) are complicated and are provided with bladder-like expansions.

That the Hirudinei are true annelids and not segmented Plathelminthes is based upon the view that their cœlom is reduced by ingrowth of parenchyma and altered to canals connected with the vascular system. At any rate the ventral and lateral vessels are to be regarded as remnants of a cœlom. In *Clepsine* there are the dorsal and ventral blood-vessels of the Chætopoda and besides four longitudinal cœlomic sinuses connected by transverse anastomoses. The dorsal sinus encloses the dorsal blood-vessel, the ventral many of the viscera, among them the ventral nerve cord. This is also to be regarded as cœlomic, since the nephrostomes connect with it. In most Hirudinei a canal system filled with blood has arisen from the cœlom and blood-vessel, and in *Nephelis* is in part lacunar in character. Further relations are shown by *Acanthobdella peledina*, parasitic on fishes. This has both blood-vessels of the Oligochætes, a body cavity divided by septa and chætæ. On the other hand it is leech-like in other features; two suckers and sexual apparatus on the Hirudinean pattern.

Order I. Gnathobdellidæ.

The jawed leeches include *Hirudo medicinalis*, once extensively used for blood-letting but now little employed. *Hœmadipsa* includes land leeches, one of the terrors of travelers in the tropics. In *Nephelis* * the jaws are soft. *Macrobdella* * includes our largest native species.

Order II. Rhynchobdellidæ.

Without jaws. The CLEPSINIDÆ mostly feed on snails and fishes. *Clepsine* * in our waters. *Hœmentaria officinalis* of Mexico is used for blood-letting ; *H. ghiliani* of South America is poisonous. The ICHTHYOBDELLIDÆ, cylindrical, occur in salt and fresh water, parasitic on fishes. *Ichthyobdella*,* *Pontobdella*,* marine ; *Piscicola*, fresh water.

Class IV. Polyzoa (Bryozoa).

In external appearance the Polyzoa closely resemble the hydroids, so that the inexperienced have difficulty in distinguishing them. Like them by budding they form colonies which are either gelatinous or calcareous incrusting sheets or assume a more bush-like character. Further they have a crown of ciliated tentacles which can be spread out or quickly retracted. In internal characters the two groups are greatly different. The Polyzoa have a complete alimentary canal, with its three divisions, which is bent upon itself so that the anus lies near the mouth. The central nervous system lies between mouth and anus, and the single pair of nephridia empty by a common opening. Beyond this it is difficult to go, since the two groups of Polyzoa—Endoprocta and Ectoprocta—differ so widely that one may doubt whether they belong together. The Entoprocta have no cœlom, and resemble in this respect the Rotifera; the Ectoprocta are true Cœlhelminthes and by way of *Phoronis* show resemblances to the Sipunculoida and so to the Annelida.

Sub Class I. Entoprocta.

The single individuals of the Entoprocta (fig. 294) are shaped like a wine-glass and are placed on stalks which rise from (usually) creeping stolons. The circle of tentacles, arising from the edge of the cup, enclose the peristomial area in which are both mouth and anus, and between these the excretory and reproductive organs open. The space between the horseshoe-shaped intestine and the body surface is completely filled by a parenchyma containing muscle cells, and correspondingly the excretory organs are protonephridia. In our fresh-water *Urnatilla gracilis* * these organs are branched and begin with flame cells. *Pedicellina* * and *Loxosoma,* marine.

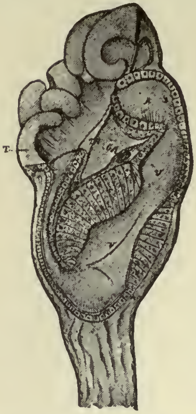


Fig. 294.—*Loxosoma singulare.* (After Nitsche.) Single individual in optical section. *A*, rectum; *Ga*, ganglion; *J*, intestine; *T*, tentacles; *V*, stomach.

Sub Class II. Ectoprocta.

In the Ectoprocta there is a spacious, often ciliated, cœlom between the alimentary canal and skin, so that these are separated and have a certain amount of independence (fig. 295). On this account has arisen a peculiar method (wholly indefensible morphologically) of treating them as two individuals, *polypid*, the intestine and tentacles; *cystid* the rest, especially the body wall and skeleton.

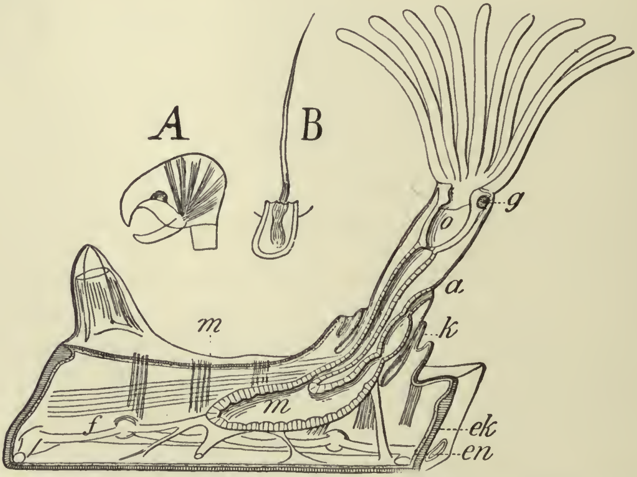


Fig. 295.—*Flustra membranacea* (after Nitsche), a single animal. *a*, anus; *ek*, ectocyst; *en*, entocyst; *f*, funiculus; *g*, ganglion; *k*, collar which permits complete retraction; *m*, stomach, also dermal muscular sac; *o*, œsophagus. *A*, avicularium; *B* vibracularium of *Bugula*. (After Claparède.)

The cystid is cup-shaped or saccular. It consists of an endocyst—the body wall—and an ectocyst—a cuticular skeleton, usually strongly calcified, secreted by the ectoderm. The surface of the entocyst is always covered by the ectocyst only on the basis and side walls; the peripheral end remains soft and forms a sort of collar into which the tentacles and adjacent parts of the cystid can be retracted. In the ectocyst there is, as will be seen, a larger or smaller opening which in many species (Chilostomata) can be closed by a lid (operculum). The circle of tentacles surrounds the mouth alone, while the anus is outside near the collar. The strongly bent alimentary canal extends into the cystid and is bound at its hinder end by a cord, the funiculus, to the base of the cystid. Ganglion and nephridia lie between the mouth and anus. The gonads arise from the epithelium of the cœlom, the testes usually on the funiculus, the ovaries on the wall of the cystid.

Hundreds and thousands of individuals form colonies (fig. 297) in which cystid abuts against cystid. The cœlom of adjacent cystids may be distinct or a wide communication may exist. The colonies grow by budding; in the Gymnolæmata a part of a cystid becomes cut off as a daughter cystid in which the polypid—alimentary tract and tentacles—arises by new formation; or (Phylactolæmata) the bud anlage of the polypid arises before the first appearance of the cystid.

Division of labor or polymorphism is common. Besides the animals already described, which are primarily for nourishment, three other individuals may occur, ovicells, vibracularia, and avicularia. All three are cystids which have lost the polypid. The ovicells are round capsules which serve as receptacles for the fertilized eggs. The vibracularia (fig. 295, *B*) are long tactile threads; the avicularia (fig. 295, *A*) are grasping structures of uncertain function. They have been seen to seize small animals and hold them until decay set in. It is possible that the fragments serve as food for the polypids. The avicularia have the form of a bird's head, the movable lower jaw being a modified operculum.

Under unfavorable conditions a polypid in a cystid may break down and be lacking for some time until better relations cause its new formation. Besides in the depopulated cystids there may appear statoblasts, lens-shaped many-celled internal buds enveloped in a firm envelope which form a resting stage for the preservation and distribution of the species. Each statoblast is surrounded by a girdle of chambers which by drying become filled with air, causing the statoblast to float when it again comes into water. From the statoblast a smaller polyzoon escapes which develops a new colony. The statoblasts are adaptations to the conditions of fresh-water life and occur only in the Phylactolæmata.

Order I. Gymnolæmata (Stelmatapoda).

The tentacles in a ring around the mouth. The numerous species are almost exclusively marine and are abundant on every coast. In the

CHILOSTOMATA the cystids can be closed by an operculum: *Gemmellaria,** *Cellularia,** *Bugula,** *Flustra** (fig. 295), *Eschara.** The CYCLOSTOMATA have tubular cystids without an operculum. *Crisia,** *Tubulipora,** *Hornera.** In the CTENOSTOMATA the cystid is more calcareous and the opening is closed by a folded membrane. *Alcyonidium,** *Vesicularia*, *Valkeria,** *Paludicella** (fresh-water).

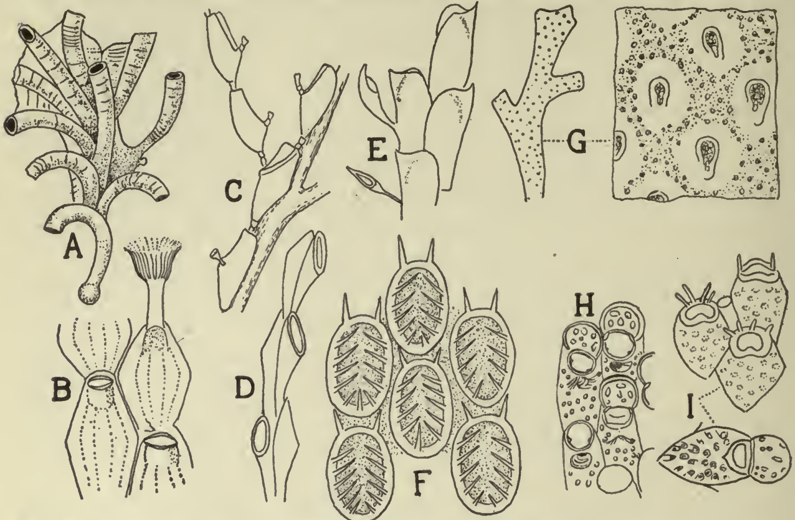


Fig. 296.—American gymnolæmatous Polyzoa. (After Busk, Hincks, Norman, and Verrill.) *A*, *Tubulipora flabellaris*, young; *B*, *Flustrella hispida*; *C*, *Eucratea chelata*; *D*, *Gemellaria loricata*; *E*, *Kinetoskias smitti*; *F*, *Membranipora spinifera*; *G*, *Porella lœvis*; *H*, *Lepralia americana*: *I*, *Cribillina puncturata.*

Order II. Phylactolæmata (Lophopoda).

Tentacles borne on a horseshoe-shaped lophophore extending on either side of the mouth, the tentacles on its margins. All are fresh-water species. *Pectinatella,** *Lophopus* (fig. 227), *Plumatella.**

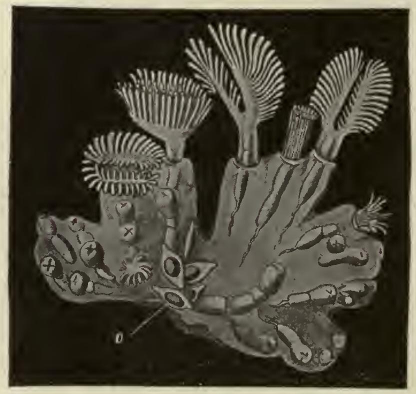


Fig. 297.—Small colony of *Lophopus crystallinus* (after Kraepelin), with young and old, some extended, others more or less retracted. *o*, statoblasts.

Class V. Phoronidea.

The single genus *Phoronis** occurs on our eastern shores. The animal was first placed among the Chætopoda on account of its worm-like body situated in a chitinous tube like many sedentary annelids. Then it was placed in the Polyzoa, with which it is more nearly related. The young, described as Actinotrocha, is a modified trochophore with the mouth overhung by a large hood and the postoral band of cilia drawn out into a series of fingers which become the tentacles of the adult; the anus is terminal. At the time of metamorphosis this larva becomes doubled on itself by a complicated process, so that the alimentary canal is U-shaped and the anus is near the mouth, while the tentacles are borne on a horseshoe-shaped basis around the mouth.

Class VI. Brachiopoda.

On account of the bivalve calcareous shells the Brachiopoda were long regarded as molluscs, but later the fact that the valves are not paired as in the lamellibranchs, but are dorsal and ventral, that the nervous system, the excretory and reproductive organs, the body cavity, and the development resemble those of the annelids rather than those of the molluscs, led to their recognition as a distinct class allied to the former group.

The body has a greatly shortened long axis (fig. 298) and in consequence a transversely oval visceral sac. In most a stalk (*st*) for attachment arises from the posterior end. From the anterior side two folds, the mantle lobes, extend forwards (*p*), one ventral, the

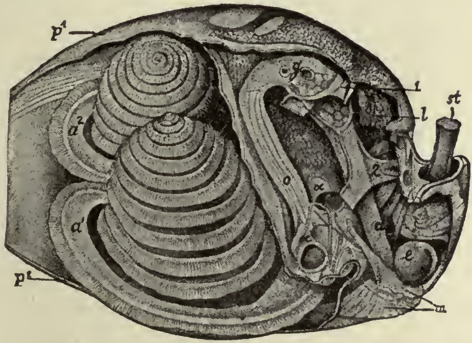


Fig. 298.—Anatomy of *Rhynchonella psittacea*. (After Hancock.) a', left, a^2, right arm; α, opening into the cavity of the arm: *d*, intestine; *e*, blind end of the intestine; *g*, stomach with liver; *m*, adductors and divaricators of shell; *o*, œsophagus; p', p^2, dorsal and ventral mantle lobes; *st*, stalk; *1*, *2*, first and second septum, on the second a nephrostome.

other dorsal, their free edges bearing bristles. Each mantle secretes a shell largely composed of carbonate and phosphate of lime. In a few the dorsal and ventral shells are similar, but usually the ventral valve (in *Crania* attached directly without the intervention of a stalk) is more strongly arched and has an opening at the posterior end for the passage of the stalk (figs. 299, 300). The flatter dorsal valve frequently bears a characteristic feature in the skeleton of the arms (fig. 300) which, when present, has greatly different expression. Its basis consists of two calcareous rods which, bilaterally symmetrical, project downwards from the dorsal valve. These may be connected by a curved transverse band, and from their ends a spiral process may extend on either side. This apparatus supports the spiral arms. When closed the valves completely enclose the body. When they open the gape is anterior,

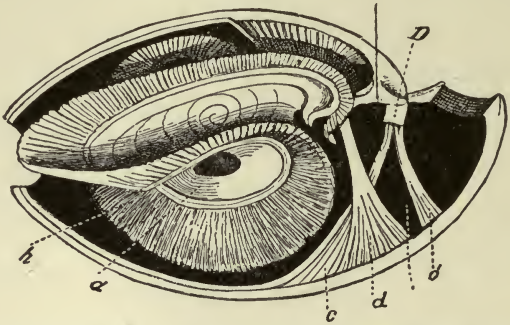


FIG. 299.—*Waldheimia flavescens.* (From Zittel.) Shell with arms and muscles. *a*, arm with fringed border (*h*); *c*, *c'*, divaricators; *d*, adductors; *D*, hinge process (the vertical line shows position of hinge).

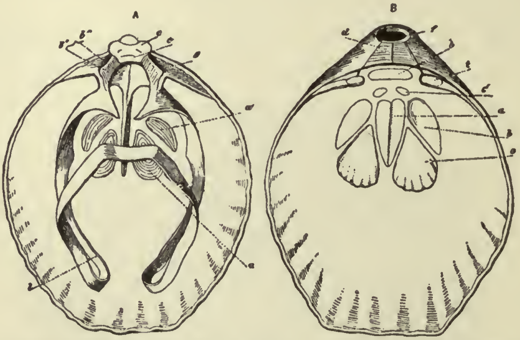


FIG. 300.—*Waldheimia flavescens.* (From Zittel.) *A*, dorsal, *B*, ventral valve; *a*, *b*, *c*, impressions of muscular insertions; *a*, adductors; *b''*, adjustors (stalk muscles); *c*, *c'*, divaricators; *s*, hinge groove of upper valve in which the tooth (*t*) of the lower valve passes; *l*, support of arms; *d*, deltidium; *f*, foramen for stalk.

the posterior parts remaining in contact. At this part, except in the Ecardines, a hinge is developed just in front of the posterior margin, consisting of projections (teeth) in the ventral valve which fit into corresponding grooves in the dorsal. Opening and closing the valves are, contrary to what occurs in Lamellibranchs, active processes, accomplished by appropriate divaricator and adductor muscles (fig. 299). These produce scars on the shell, important in the study of fossil forms.

The usually spirally coiled arms, which lie right and left of the mouth and which give the name to the class, fill most of the shell. On the outer side of the spiral axis runs a longitudinal groove which reaches to the tip of the arms and is bounded by a row of small tentacles. By means of cilia on tentacles and groove food is brought to the mouth. These arms strongly resemble the lophophore of a phylactolæmate Polyzoan, which only needs extension and coiling to produce this condition. In development the arms of the Brachiopod pass through a lophophore stage.

In the body there is a body cavity which extends into both mantle folds. It encloses alimentary tract, gonads, and liver, and is divided into right and left halves by a dorsal mesentery supporting the intestine. Each half in turn is divided by incomplete septa into anterior, middle, and posterior divisions recalling those of *Sagitta* (p. 296). If the arrangement of the septa is not so clear as in that form, it is to be explained by the shortening of the long axis and the twisting of the alimentary tract. This latter consists of œsophagus, stomach, which receives the liver ducts, and intestine, which in some species terminates blindly.

The gonads are chiefly in the mantle lobes. The sexual cells pass outwards through the nephridia, which begin in one cœlomic pouch with a wide nephrostome, perforate the septum, and open to the exterior in the next somite. Since usually there are two septa, two pairs of nephridia may occur, but one is usually degenerate. The nervous system consists of an œsophageal ring with weak dorsal ganglion, which sends nerves into the arms, and a stronger ventral mass representing the ventral chain. The heart lies dorsal to the stomach.

In development the brachiopods recall both *Sagitta* and the Annelida. They resemble *Sagitta* in that in *Argiope* the cœlom arises by outgrowths from the archenteron, divided by septa into three pairs of pouches. They are annelid-like in the form of larva and in the presence of chætæ which are formed in separate follicles. In an earlier period of the earth brachiopods were so numerous in species and individuals that they are among the most important fossils in the determination of geologic horizons.

Now there are but few species, some inhabitants of the greatest depths of the sea.

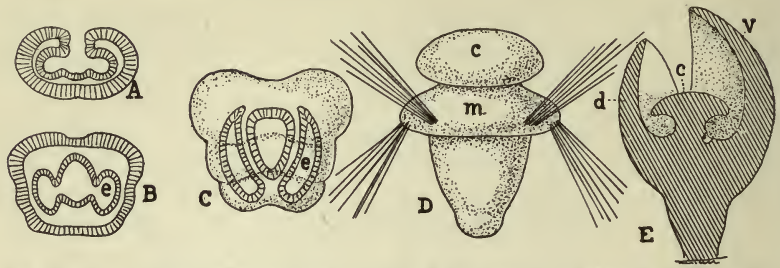


FIG. 301.—Development of brachiopod. (After Kowalevsky.) *A*, gastrula with early enterocœlic pouches; *B*, closure of blastopore; *C*, cœlom separated, body annulated; *D*, cephalic disc and mantle developing, the latter with long setæ; *E*, attached embryo, the mantle lobes folded over cephalic disc (setæ omitted). *c*, cephalic disc; *d*, dorsal lobe of mantle; *e*, enterocœle; *m*, mantle; *v*, ventral mantle lobe.

Order I. Ecardines.

Hinge absent; valves similar when the stalk passes out between them (*Lingula* *), or unequal when the ventral is perforated by the stalk (*Discina*) or when the animal is directly attached by the shell (*Crania*).

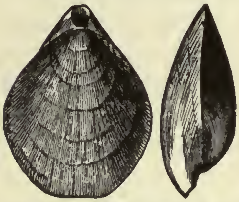


FIG. 302.—*Terebratulina septentrionalis.**

Order II. Testicardines.

Hinge present, valves unequal, the ventral perforated by the stalk; anus degenerate. *Rhynchonella*,* *Terebratulina** in our colder waters. *Spirifer*, *Orthis*, *Pentamerus*, *Atrypa*, important fossil genera.

Summary of Important Facts.

(1) The CŒLHELMINTHES are characterized by a well-developed body cavity (cœlom).

(2) The CHÆTOGNATHI are hermaphroditic worms with three pairs of cœlemic pouches, with fins, and bristle-like jaws.

(3) The NEMATODA are mostly diœcious, usually parasitic elongate worms, with cylindrical unsegmented body, with nerve ring (no ganglia), paired excretory organs, and tubular gonads.

(4) The most important species parasitic in man are *Ascaris lumbricoides* in the small intestine, *Oxyuris vermicularis* in the large intestine, the blood-sucking *Ankylostoma duodenalis*, and the notorious *Trichina spiralis.* In hot climates occur *Filaria sanguinis hominis* and *Dracunculus medinensis.*

(5) The GORDIACEA have mesenteries and splanchnic mesoderm; they are parasitic in insects.

(6) The ACANTHOCEPHALI lack alimentary tract, have a spiny proboscis and a very complicated reproductive apparatus. The adults are parasitic in vertebrates, the young in arthropods.

(7) The CHÆTOPOD ANNELIDS have segmented bodies, the segmentation showing itself in ringing of the body wall and in the separation of the cœlœm into a series of pouches by transverse septa and the metameric arrangements of blood-vessels, ganglia, and excretory organs.

(8) The CHÆTOPODA are distinguished from other annelids by the chætæ (usually four bunches in a somite) arising in special follicles. The chætæ are few in the hermaphroditic Oligochætæ, numerous and borne on special parapodia in the Polychætæ.

(9) The GEPHYRÆA are closely related to the Chætopoda. They are saccular, with a crown of tentacles or well-developed preoral lobe. They have largely or entirely lost the segmentation. Evidence of segmentation appears in some cases in development and in the ventral nerve cord and nephridia.

(10) The HIRUDINEI are hermaphroditic Annelida which lack chætæ but have sucking discs. Their flattened bodies, rudimentary cœlom, and rich body parenchyma give them a certain similarity to the Plathelminthes.

(11) The Hirudinei have either a protrusible pharynx (Rhynchobdella) or three toothed jaws (Gnathobdella). To the latter belongs the medicinal leech (*Hirudo medicinalis*).

(12) The POLYZOA are like the Hydrozoa in being colonial and having a circumoral crown of tentacles. They are distinguished by the complete alimentary canal, the large cœlom, and the ganglionic nervous system.

(13) The PHORONIDEA are closely like the Polyzoa.

(14) The BRACHIOPODA have a bivalve shell, the valves being dorsal and ventral.

(15) The body cavity is divided by two septa into three (paired) chambers, of which one, rarely two, are provided with nephridia.

(16) Most brachiopods are attached by means of a stalk. They are divided into Ecardines, without a hinge and with anus, and Testicardines, with a hinge and no anus.

PHYLUM V. ECHINODERMA.

The Echinoderma are separated from most other animals by their radial symmetry, but recall in this respect the Cœlenterata, a fact which led to their inclusion by Cuvier in the group 'Radiata,' a view of their relationships which was set aside by Leuckart on account of their different structure, especially the presence of a cœlom. In fact the radial symmetry of the echinoderms has a different value, for while in the Cœlenterata the number four or six (apparently derived from four) is fundamental, Echinoderma are, with few exceptions, five-radiate. Further, the radial symmetry of the Cœlenterata is primitive, that of the Echinoderma, as development shows, is derived from the bilateral type. In other words, the echinoderms have descended from bilateral, possibly worm-like, ancestors.

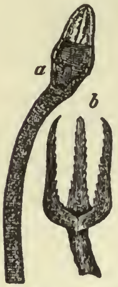


FIG. 303. — Pedicellaria, closed and open

The structure of the integument gives these animals a characteristic appearance. In the mesoderm under the epithelium calcareous plates arise, forming a body armor or test, and since these are usually produced into spines, they have given the name Echinoderma, spine skin, to the group. This mesodermal skeleton at times becomes degenerate, as in the Holothurians (it rarely entirely disappears as in *Pelagothuria*), but even then shows itself as spicules and 'wheels' of lime. The sphæridia and pedicellaria (fig. 303)—not always present—are characteristic appendages of the integument. The first are sense organs; the latter are usually stalked forceps-like grasping structures with calcareous skeleton. In life they are active and apparently either clean the skin or are defensive.

Certain plates possess a morphological interest since they appear early in many larvæ, and in the adults of different classes can be recognized in similar positions. In the neighborhood of the arms are five basalia, interradial in position, farther five radialia ('apical skeleton') and five interradial 'oralia' around the mouth.

Not less characteristic than the skeleton is the ambulacral (or water-vascular) system (fig. 304). This begins usually externally and then ordinarily by a calcareous plate, the madreporite, which is perforated with fine pores and serves for the entrance of sea water. The water passes into a canal which, on account of its calcified walls in the starfish (fig. 305), is called the stone canal and leads

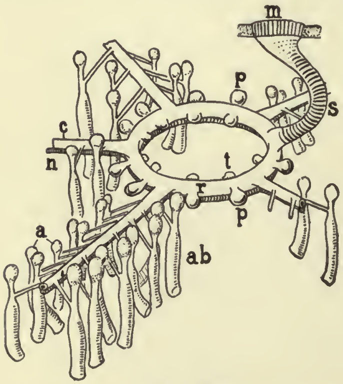


FIG. 304.

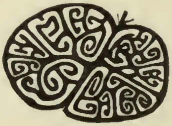


FIG. 305.

FIG. 304.—Water-vascular system of starfish (orig.). *a*, ampullæ; *ab*, ambulacra; *c*, radial canal; *m*, madreporite; *n*, radial nerve; *p*, Polian vesicle; *r*, ring canal, beneath it the nerve ring; *s*, stone canal; *t*, racemose vesicle.

FIG. 305.—Transverse section of stone canal of *Astropecten aurantiacus*. (After Ludwig.)

orally to a ring canal around the mouth. The ring canal bears usually several (up to five pairs) Polian vesicles, which, with Tiedemann's vesicles of the starfishes, are now regarded as appendages which, like lymph glands, produce the leucocytes. From the ring canal radiate five radial canals which give off right and left in pairs the ambulacral canals. These in turn connect with the ambulacra and ampullæ, the highly characteristic locomotor organs of the echinoderms. An ambulacrum is a muscular sac which can be distended and lengthened by forcing in fluid from the ambulacral vessels, on the other hand can be retracted and shortened by its muscles. The ampulla is a sac connected with the ambulacrum and projecting into the body cavity. In locomotion the animal extends its ambulacra, anchors them by the sucking disc at the tips, and then pulls the body along by contraction of the ambulacral muscle. In the sessile crinoids and the ophiuroids (which move by their snake-like arms) the ambulacra are not locomotor but tactile in function, lacking suckers and ampullæ. So among the holothurians and sea urchins the ambulacra are in many places replaced by tentacles. Frequently each radial canal ends in an unpaired tentacle with olfactory functions.

The arrangement of the ambulacral system conditions the arrangement of other organs. Alongside the stone canal is a saccular organ formerly called the 'heart,' but now regarded as a lymphoid gland (ovoid gland, paraxon gland). Ring and radial canals are accompanied by corresponding blood canals, with which are often associated two vessels to the alimentary canal. There is a similar nerve ring and radial nerve, frequently in the ectoderm, to which may be added an enterocœlic or apical nervous system, possibly of peritoneal origin.

The courses of the radial vessels and nerves mark out five chief lines in the animal, the radii; between them come the secondary radii or interradii. The stone canal, madreporite, and lymphoid gland are interradial in position, as are the gonads, usually five single or five pairs of racemose glands; in some cases but one is present. The gonads are supported in the spacious cœlom by special bands, while mesenteries support the alimentary tract and its derivatives.

Respiratory organs are represented by very various structures: branchiæ, or thin-walled outpushings of the cœlom, either around the mouth, as in Echinoidea, or on the aboral surface, as in the Asteroidea, the bursæ of the Ophiuroidea, the branchial trees of the Holothuroidea and the various parts of the ambulacral system.

The Echinoderma are exclusively marine, occurring in large numbers even in the deepest seas. Many groups, like the Crinoids, are largely bathybial, others frequent rocky coasts. At the period of reproduction the urchins, starfish, and holothurians frequent the shallow waters, passing their sexual cells into the sea, where fertilization occurs. In some, however, the young are carried about in brood cases until the earlier developmental stages are past.

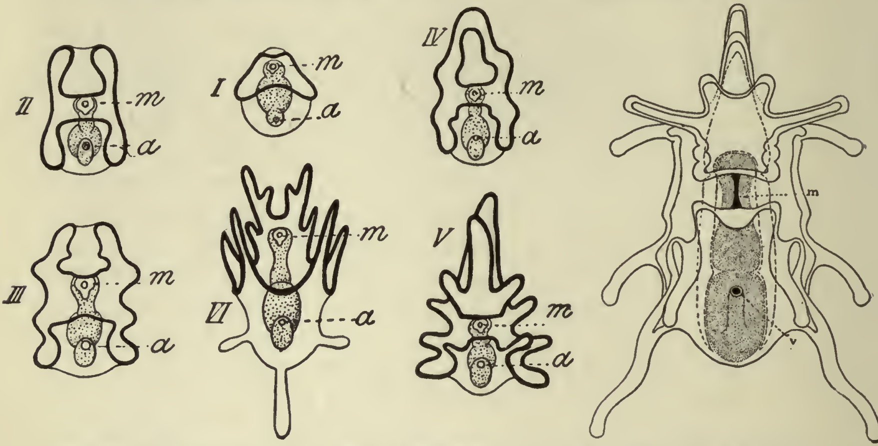


FIG. 306.—Echinoderm larvæ. (After J. Müller.) *a*, anus; *m*, mouth; the black line, the course of the ciliated bands. *I*, form common to all; *II*, *III*, developmental stages of auricularia (Holothurian); *IV*, *V*, stages of the Asteroid bipinnaria; *VI*, pluteus of a spatangoid; *VII*, larva (Brachiolaria) of *Asterias* (orig.). *m*, mouth; *v*, vent.

Where there is no brood pouch the young escape from the egg as larvæ which swim at the surface, and are distinguishable from the adults (fig. 306, *I*) by their soft consistency, transparency, and bilateral symmetry. By the development of lobe-like processes and slender arms supported by calcareous rods the larvæ assume the most different and bizarre shapes (plutei of echinoids and ophiuroids, brachiolaria and bipinnaria of asteroids, auricularia of holothurians), all of which can be referred back to a common type with tri-regional alimentary tract and a ciliated band around the mouth, strikingly resembling tornaria, the larva of *Balanoglossus*. The different appearances of the larvæ are due to the drawing out of the ciliated band into lobes and arms, and also to its becoming broken into parts which unite themselves into complete rings (fig. 306, *V*).

The metamorphosis of the bilateral larva into the radial adult is very complicated. It begins early with the formation of outgrowths from the archenteron (fig. 307), which become separated and form the anlagen of the cœlom and ambulacral system. This becomes divided, and one portion develops itself as a ring around the œsophagus, the future ring canal, and from this five outgrowths, the radial canals, arise. Since these canals, as they grow out, carry the body walls before them, the arms in the starfishes, which show the process most clearly, arise as outgrowths which recall buds (fig. 308). This has given rise to one view which regards the arms as individuals, the whole body (and hence that of all echinoderms) as a colony of five individuals. According to this the development would be a kind of alternation of generations, the larva being the asexual generation which by budding produces the colony. Yet this view does not agree with the actual relations, since it draws an untenable contrast between the larva and the perfect echinoderm. The most important organs of the former are carried over into the latter, and the echinoderm brings the anlagen to further development. In the insects many features which are lacking or incompletely developed in the larva are developed in the course of the metamorphosis. There is a metamorphosis in the echinoderms as in insects. It is a question as to which group of Echinoderma is the most primitive, but ease of treatment makes it best to begin with the Asteroidea.

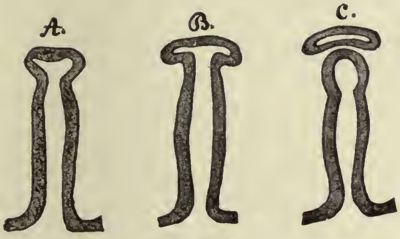


Fig. 307.

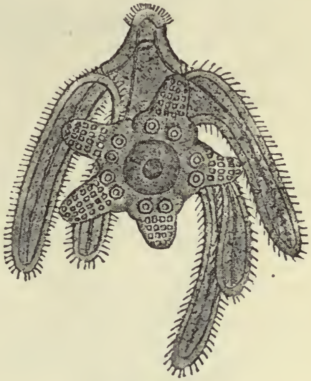


Fig. 308.

Fig. 307.—Formation of the cœlom in *Echinus*. (From Korschelt and Heider.) *A*, first anlage of cœlom; *B*, later stage; *C*, complete constriction of cœlom (vaso-peritoneal vesicle) from archenteron.

Fig. 308.—Formation of Ophiuran from the pluteus larva. (After Müller, from Korshelt-Heider.)

Class I. Asteroidea (Starfish).

Two parts can be recognized in the body of a starfish, a central disc and the arms, usually five in number, which radiate from it (fig. 316). The relations in which these parts stand to each other vary between two extremes. In many starfish the arms play the chief rôle and the disc appears as only their united proximal ends (figs. 309, 310). On the other hand the disc may increase at the expense of the arms, absorbing these in its growth so that they form merely the angles of a pentagonal disc (fig. 311).

In both arms and disc two surfaces are recognized, oral and aboral, which pass into each other, usually without a sharp margin. In the normal position the oral side is downwards and has in the centre the mouth and radiating from it to the tips of the arms the five ambulacral grooves. On the aboral surface is the anus (when not degenerate) near the centre, and excentric from it in an interradius is the madreporite (in many armed species two to sixteen radii may have madreporites).

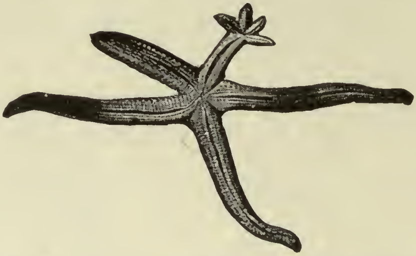


Fig. 309.—Comet form of *Linckia multiflora.* (From Korschelt-Heider.) One of the arms is producing a new animal by budding.

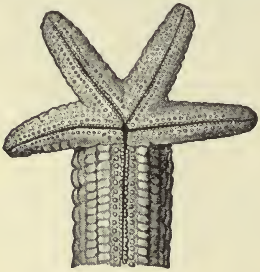


Fig. 310.

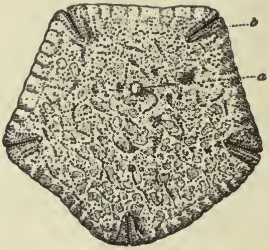


Fig. 311.

Fig. 310.—*Ophidiaster ehrenbergi.* (After Haeckel). Comet form; one of the original arms shown only in part.

Fig. 311.—*Culcita pentangularis*, aboral view. (From Ludwig.) *a*, madreporite; *b*, reflexed end of ambulacral grooves.

A line passing through the madreporite and the opposite arm divides the body into symmetrical halves. This ray is frequently spoken of as anterior, since in the irregular sea urchins (Spatangoids) the homologous arm is clearly anterior, while the madreporic interradius is posterior. This plane of symmetry does not correspond with that of the larva. The two rays on either side of the madreporite form the bivium, the three others the trivium.

The skin is everywhere protected by large and small plates jointed together. These make a dry starfish hard and stiff, but in life it is extremely flexible, the arms can be bent in any direction, and the animal can work its way through narrow openings. Of the skeletal pieces the ambulacral plates need special mention.

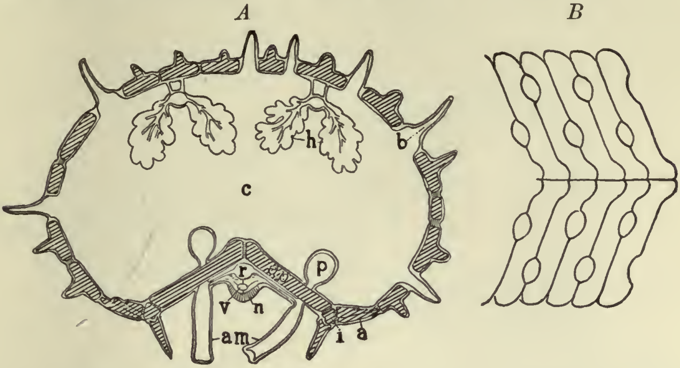


FIG. 312.—*A*, cross-section of starfish arm (orig.). *a*, adambulacral plates; *am*, ambulacra; *ap*, ambulacral plates; *b*, branchiæ; *c*, cœlom; *h*, hepatic cæca; *i*, interambulacral plates; *n*, radial nerve; *p*, ampulla; *r*, radial canal; *v*, radial blood-vessel. *B*, ambulacral plates, ventral view, showing the ambulacral pores between.

These form the roofs of the ambulacral grooves, and between them are openings, the ambulacral pores, through which connexion is made between the ambulacra and ampullæ. In each arm the pairs of ambulacral plates meet above the groove like the rafters of a roof. Laterally each ambulacral plate abuts against a small interambulacral plate, bearing usually movable spines. Beyond these comes the adambulacral plates, and then those of the aboral surface. Each ambulacral area terminates at the tip of the arm with an unpaired (ocular) plate.

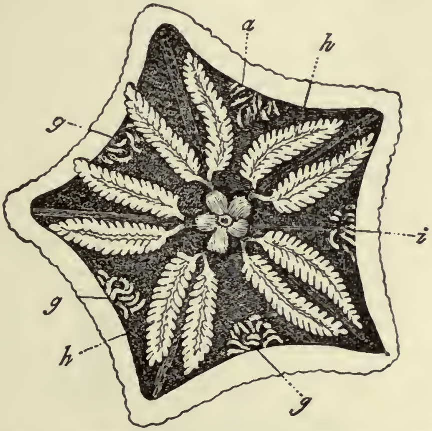


FIG. 313.—*Asteriscus verruculatus*, aboral surface removed. (After Gegenbaur.) *g* gonads; *h*, hepatic cæca; *i*, stomach with anus.

The organs lie in part in the cœlom, in part in the ambulacral grooves. The alimentary tract is in the cœlom and extends straight upward from the mouth to the aboral surface, where it ends with an anus or is entirely closed (figs. 313, 314). By a constriction it is divided into a larger, lower cardiac portion and a smaller, upper pyloric division. From the latter arise five hepatic ducts which connect with five pairs of hepatic glands lying in the arms. The cardiac division gives origin to five gastric pouches which can be protruded from the mouth or retracted by appropriate muscles. The gonads are five pairs of racemose glands lying in the basis of the arms and opening interradially between the arms. Lastly, the stone canal, extending from the aboral madreporite to the ring canal, and the lymphoid gland lie in the cœlom.

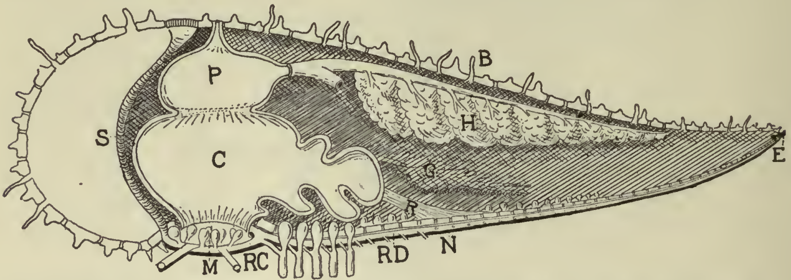


FIG. 314.—Section through ray and opposite interradius of a starfish (orig.). *B*, branchiæ; *C*, cardiac pouch of stomach; *E*, eye spot; *G*, gonad; *H*, 'liver'; *M*, mouth; *N*, radial nerve; *P*, pyloric part of stomach; *RC*, ring canal; *RD*, radial canal of water-vascular system; *S*, stone canal.

The radial nerve, canal, and blood-vessel lie in the roof of the ambulacral groove between the ambulacra. The nerve ends at the tip of the arm in a compound eye spot colored with red or orange pigment which experiment shows is sensitive to light. A second nerve has been described lying in the cœlom of the arm. The ambulacral system corresponds with the foregoing description

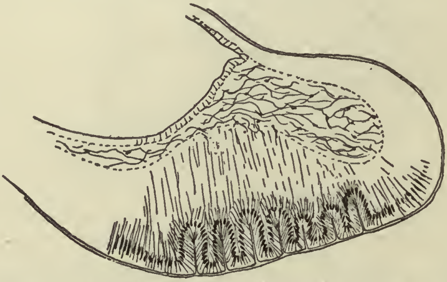


FIG. 315.—Longitudinal section of eye of *Asterias*. (Orig.)

(p. 330), the ampullæ as well as the five or more Polian and Tiedemann's (racemose) vesicles projecting into the cœlom.

Since the arms contain nearly all important organs, the physiological independence of these is easily understood. Arms broken off not only live, but regenerate first the disc and then new arms which appear at first like small buds (comet form, figs. 309, 310). This separation of arms may occur through accident, or it may be, and not infrequently is, produced by the animal itself.

Examples of species with well-developed arms and ambulacra in four rows are furnished by the ASTERIDÆ, represented on our shores by the five-finger *Asterias** and *Leptasterias*,* and *Heliaster** with numerous arms. In the SOLASTERIDÆ the ambulacra are two-rowed; arms sometimes numerous. *Pythonaster* (fig. 316). In the ASTERINIDÆ the arms are short or the body is pentagonal, no large plates on the margins of the arms. *Asteriscus* (fig. 313). In other forms (*Culcita*,* fig. 317, *Hippasteria*,* *Ctenodiscus**) the body is more or less pentangular, the margin being covered with large plates.

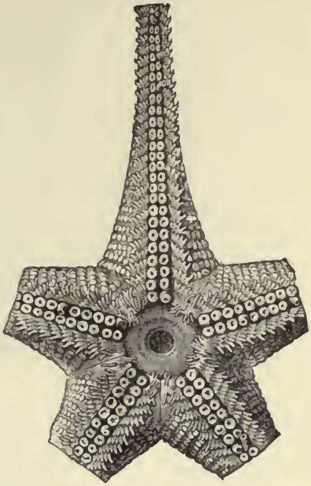


FIG. 316 — *Pythonaster murrayi*. (After Sladen.) Aboral view showing ambulacral grooves.

Class II. Ophiuroidea (Brittle Stars).

In these the animal consists, as in the Asteroidea, of disc and arms, the latter sometimes branched, but the internal anatomy is different. The ambulacral plates have been drawn inside the arm and each pair fused to a large 'vertebra' (fig. 317). As a result the cœlom of the arms is greatly reduced, the hepatic cæca are lacking, and the alimentary canal, which lacks an anus, is confined to the disc. By the ingrowth of ventral plates the ambulacral grooves are converted into tubes, and the ambulacra, which lack sucking discs, are tactile organs, locomotion being effected by the snake-like motion of the arms. The madreporite is on the ventral sur-

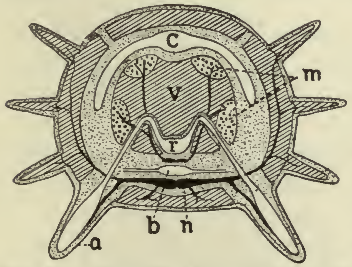


FIG. 317. — Section of Ophiuroid arm (orig.). *a*, ambulacrum; *b*, blood vessel; *c*, cœlom; *m*, muscles of arm; *n*, nerve; *r*, radial water tube; *v*, 'vertebra' (coalesced ambulacral plates).

face. Also on the ventral surface are five slits which connect with as many bursæ, thin-walled respiratory sacs into which the sexual organs open.

In many brittle stars (*Ophiocnida*, *Ophiothelia*, *Ophiocoma*), especially in young specimens, there is a kind of asexual generation (schizogony), the animal dividing through the disc, the halves regenerating the missing parts. The classification is based largely on small details. In the majority the arms are unbranched (*Ophiopholis* * (fig. 318), *Ophioglypha*,* *Amphiura* *), but in the EURYALIDÆ, or basket fish, the arms are branched (*Astrophyton*,* fig. 319), but not, as usually stated, dichotomously.

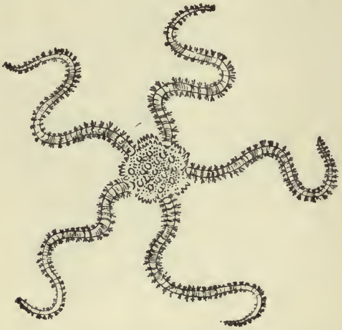


FIG. 318.

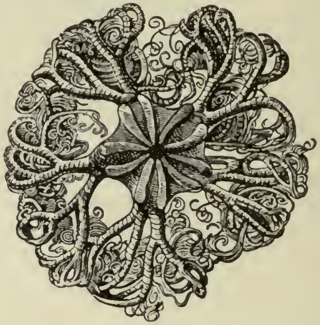


FIG. 319.

FIG. 318.—*Ophiopholis aculeata.** (From Morse.)
FIG. 319.—*Astrophyton arborescens*, basket fish. (From Ludwig.)

Class III. Crinoidea (Pelmatozoa).

The crinoids or sea lilies are on the road to extinction. In early times, especially in the paleozoic, they were very abundant, but to-day there are but few genera and species, these mostly restricted to the greater depths of the ocean, only the Comatulidæ occurring near the shore. The crinoids are attached to the sea bottom by a long stalk which contains a central canal (fig. 320). This stalk is composed of cylindrical discs and often bears five rows of outgrowths, the cirri. In the Comatulidæ (fig. 321) the adult is not thus attached, swimming about in the water with the arms or moving about on the tang. In their earlier stages these animals have a stalk (fig. 322), passing through a *Pentacrinus* stage, a proof that the fixed condition was the primitive one. In these forms, when the separation takes place, one joint of the stalk with its cirri remains attached to the animal, as the centrodorsal united with the lowest cup plates, the infrabasals (fig. 321).

On the upper joint of the stalk is a cup-shaped body (theca) the edges of which bear five or ten (usually branched) arms. The

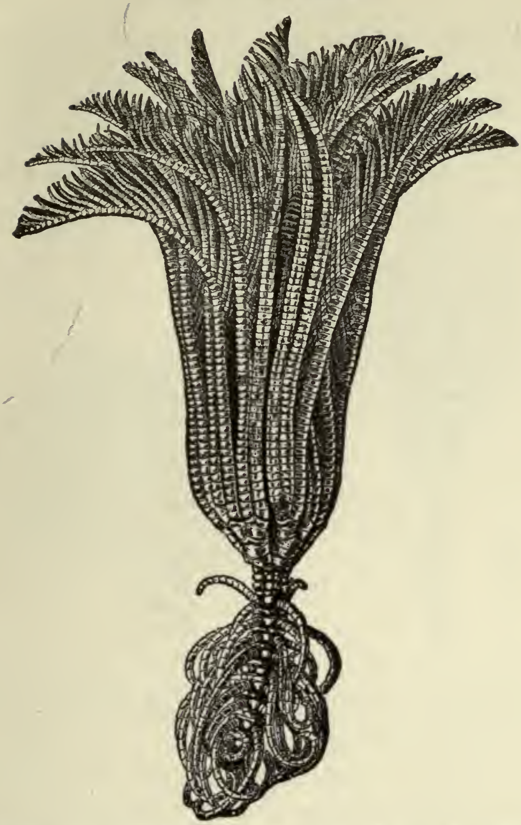


Fig. 320.—*Pentacrinus macleayanus.* (After Wyville Thompson.)

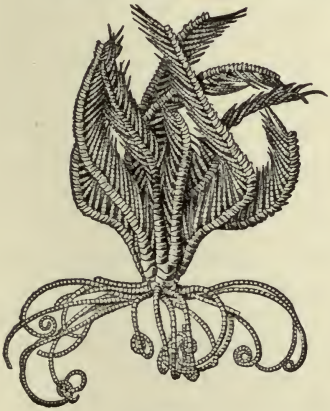


Fig. 321.

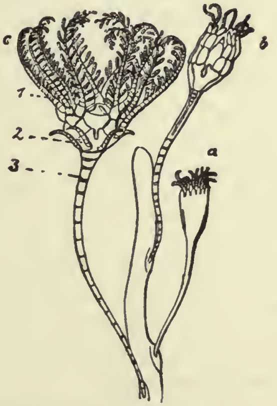


Fig. 322.

Fig. 321.—Adult of *Antedon macronema.* (After Carpenter.)
Fig. 322.—Different *Pentacrinus* stages (*a*, *b*, *c*) of *Antedon rosacea.* *1*, arms; *2*, cirri; *3*, stalk.

walls of the theca are covered with polygonal calcareous plates. Usually the stalk bears five plates, the basalia, and then come five radialia, alternating in order with the basalia (fig. 323). In some there is a circle of infrabasalia in a line with the radialia. Frequently the elements of the arm, the brachialia, are directly attached to the radials (fig. 323). But often the arm branches once or several times dichotomously, and the first branching takes place at the base, so that the arms seem to spring from the theca. In these cases the first brachialia are considered as part of the theca and are called radialia distichalia (figs. 320, 321). From the arms arise, right and left, a row of pinnulæ, lancet-shaped processes supported by calcareous bodies in which the sexual products ripen until freed by dehiscence (fig. 325).

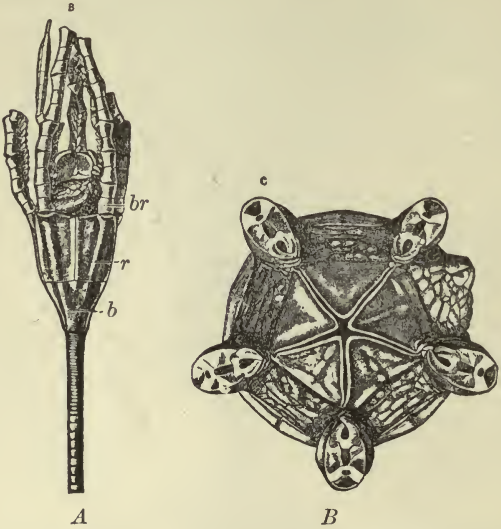


Fig. 323.—*Hyocrinus bethleyanus.* *A*, upper end of stalk with cup, and the bases of the arms; *b*, basalia; *br*, brachialia; *r*, radialia. *B*, oral surface of cup with mouth, five oralia, and the bases of the arms.

The mouth opening, in the middle of the oral disc which closes the theca, is frequently surrounded by five radial plates, the oralia. The mouth, which in contrast to other echinoderms is directed upwards, connects with a spacious digestive tract in which œsophagus, stomach, and intestine can be distinguished. The anus is interradial and near the mouth (fig. 324). Five ambulacral grooves begin at the mouth and extend out on the arms, branching with them and extending to the tips of the pinnulæ. These are ciliated and serve as conduits to bring food to the mouth. Nervous, ambulacral, and blood systems begin with a circumoral ring. They follow the ambulacral grooves as in the asteroids, but the ambulacra

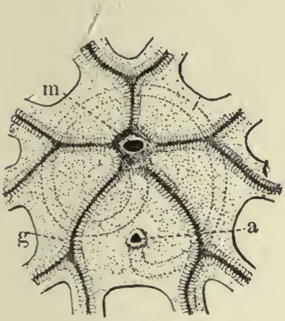


FIG. 324.

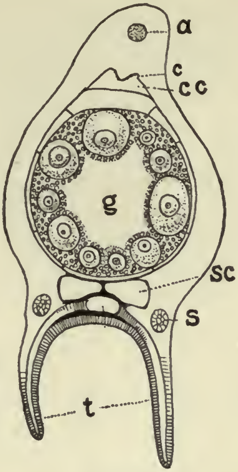


FIG. 325.

FIG. 324.—Oral area of crinoid (*Antedon*), showing by dotted lines the course of the intestine from the mouth (*m*) to the anus (*a*); *g*, ciliated grooves leading from the arms to the mouth (orig.).

FIG. 325—Cross-section of pinnula of *Antedon*. (After Ludwig.) *a*, axial nerve cord; *c*, ciliated cups; *c, c*, cœliac canal; *g*, gonad; *s*, sacculi; *sc*, subtentacular canal; *t*, tentacles.

here have no suckers nor ampullæ and are merely tactile tentacles. A typical stone canal is also lacking; in its place are five or several hundred tubules leading from the ring canal to the cœlom. Opposite their cœlomic mouths are fine pores in the oral disc through which water enters to pass through the tubules into the ambulacral system. The ambulacral nervous system is weakly developed. The enterocœle system, on the other hand, is well developed and forms the axial cord running through the brachialia and radialia to unite in a ring in the centrodorsal. A problematical organ, the so-called dorsal organ, also begins in the centrodorsal and extends up through the axis of the theca to the oral disc. It is possibly a lymphoid gland, possibly a structure for the transfer of nutriment, and is apparently homologous with the 'heart' of the starfish.

Sub Class I. Eucrinoidea.

The foregoing account applies entirely to the Eucrinoidea, which may be divided into two groups :

Order I. TESSELLATA (Palæocrinoidea). Theca with its side walls composed of immovably united thin plates ; the ambulacral grooves usually completely covered by calcareous plates. Exclusively paleozoic.

Order II. ARTICULATA (Neocrinoidea). Ambulacral grooves open, theca with compact, in part movably articulated, plates. This order left the other in the mesozoic age, and some families have persisted until now. *Rhizocrinus* * (fig. 323) and *Pentacrinus* (fig. 320), deep seas ; the COMATULIDÆ are fixed in the young, free in the adult. *Antedon* * (fig. 321).

Sub Class II. Edrioasteroidea (Agelacrinoidea).

Theca of irregular plates ; arms unbranched and lying on the theca. Possibly the ancestors of the noncrinoid echinoderms. Paleozoic. *Agelacrinus.*

Sub Class III. Cystidea.

Exclusively paleozoic ; body spherical, composed of polygonal plates. Stalk and arm structures rudimentary, sometimes lacking. The AMPHORIDA are by some regarded as ancestral of all echinoderms. *Holocystites*, *Echinosphærites* (fig. 326).

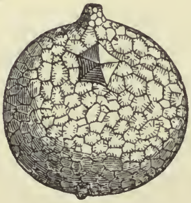


FIG. 326.

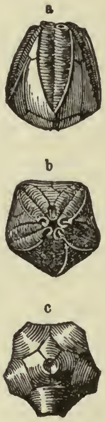


FIG. 327.

FIG. 326.—*Echinosphærites aurantium.* (From Zittel.)
FIG. 327.—*Pentremites florealis.* (From Zittel). Lateral, oral, and aboral views.

Sub Class IV. Blastoidea.

Arms lacking ; the mouth surrounded by five petal-like ambulacral areas. The group appears at end of Silurian and dies out with the carboniferous. *Pentremites* (fig. 327).

Class IV. Echinoidea (Sea Urchins).

The structure of the sea urchins is best understood in the spherical forms (figs. 328, 330). Mouth and anus lie at opposite poles of the main axis, each opening immediately surrounded by areas covered by calcareous plates, the arrangement of which varies with the family. Around the anus is the periproct, around the mouth the peristome, the latter bearing sphæridia and in the Echinoids five pairs of interambulacral gills. Between peristome and periproct the body wall is composed of calcareous plates, which, except in the Echinothuridæ, are immovably united. Aside from the extinct Palæcheinoidea the plates are arranged in twenty meridional rows, or, more accurately, in ten double rows, two rows being always intimately associated together. Five of these double rows are ambulacral, the alternating five interambulacral. Both bear small hemispherical articular surfaces on which are situated the spines, either long and pointed or swollen to spherical plates. These spines are extremely mobile and are moved by muscles so that they serve both as protecting and locomotor structures. The ambulacral plates are

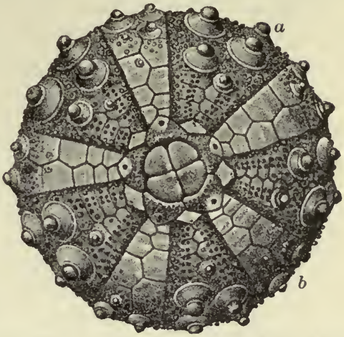


Fig. 328.—*Cœlopleurus floridanus.** (After Agassiz.) Aboral view, the spines removed to show the ambulacral (*a*) and (*b*) interambulacral areas, ending respectively in the ocular and genital plates; in the centre the four plates of the periproct.

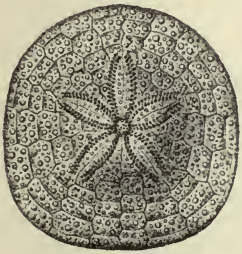


Fig. 329.

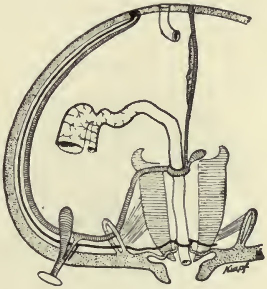


Fig. 330.

Fig. 329.—*Clypeaster subdepressus.* (After Agassiz.) Aboral view, showing the petaloid ends of the ambulacral areas.
Fig. 330.—Diagrammatic longitudinal section through a sea urchin.

distinguished from the interambulacral by the ambulacral pores by which the ambulacra on the surface are connected with the internal ampullæ. In most sea urchins the paired grouping of the pores results from the fact that a double canal extends from ampulla to ambulacrum.

In the arrangement of the ambulacra two modifications, the band form and the petaloid, occur. In the first the ambulacra are equally developed from peristome to periproct (fig. 328). In the second oral and aboral regions may be distinguished (fig. 329). In the oral region alone are locomotor feet always present, but these are so irregularly arranged that no striking figure results. In the aboral area the ambulacra are tentacular in character and are regularly arranged, their pores bounding five petal-like figures around the periproct, very distinct after removal of the spines. In the Echinoids, the Cidarids excepted, the interambulacral plates around the peristome show five pairs of notches for the gills, five pairs of thin-walled branching extensions of the body cavity.

Ambulacral and interambulacral fields both end at the periproct with an unpaired plate, the five ambulacral plates (radialia of morphology) being called ocular plates, since they often bear pigment spots formerly regarded as eyes. They are perforated by the end of the radial canal and nerve, the latter here uniting with the epithelium of the skin. The five interambulacral plates are called genital plates, since they usually contain the openings of the genital ducts. One is often madreporite as well.

The interior of the body is occupied by a spacious cœlom, to

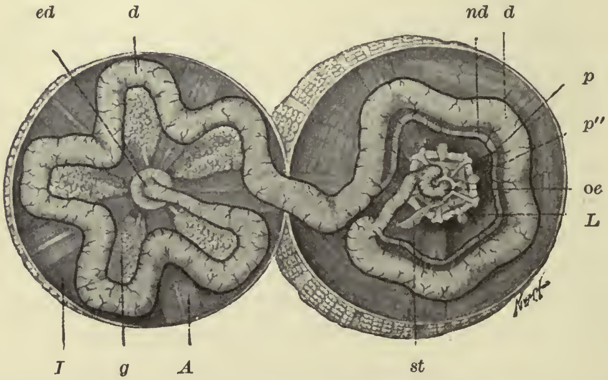


FIG. 331.—Sea urchin opened around the equator. *A*, ambulacral area; *I*, interambulacral area; *L*, lantern; *d*, intestine; *ed*, anal end of intestine; *g*, gonads; *nd*, siphon; *oe*, œsophagus; *p*, *p′*, ring canal and Polian vesicles; *st*, stone canal.

the walls of which the thin-walled alimentary tract is fastened by a mesentery. In the Clypeastroids this tract forms a simple spiral, but elsewhere it is a double spiral. It ascends from the mouth, turning once, and then, bending on itself, coils in the reverse direction to the anus (fig. 331). Usually the first portion of the canal is accompanied by a siphon, an accessory tube opening into the main tube at either end. Except in the Spatangoids the mouth is surrounded by five sharp-pointed calcareous plates, the teeth, which in the Echinoids are supported by a complicated system of levers, fulcra, and muscles, the 'lantern of Aristotle' (fig. 332).

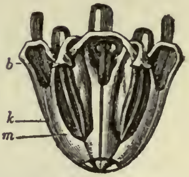


Fig. 332. — Aristotle's lantern of *Strongylocentrotus lividus*. (After Schmarda.) *b*, radulæ; *k*, alveoli; *z*, teeth.

The ring canal and the ring of the blood system lie on the lantern, the stone canal and ovoid gland ('heart') extending upwards from them (fig. 330). The blood-vascular ring gives off two blood-vessels which run along the alimentary canal, while from the ring canal arise five ambulacral or radial canals which run on the inner side of the test accompanied by nerves which radiate from a nerve ring. The gonads are five (rarely four or two) unpaired organs in the aboral half of the test, opening through the genital plates, that is, interradially as in the starfish.

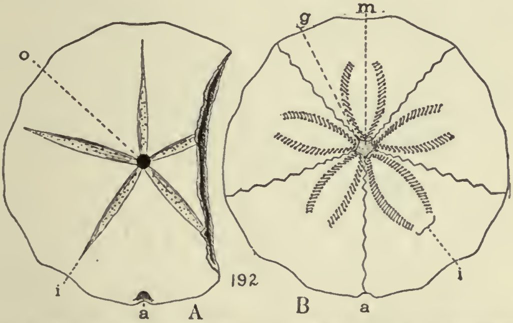


Fig. 333.—Oral (*A*) and aboral (*B*) surfaces of the sand dollar, *Echinarachnius parma*. *a*, anus; *g*, genital pores; *i*, ambulacral areas; *m*, madreporite; *o*, mouth.

Order I. Palæechinoidea.

Paleozoic forms with five ambulacral areas, the interambulacral areas containing more than two rows of plates. *Melonites*.

Order II. Cidaridea (Regulares).

Ambulacral areas band-like, body more or less spherical, mouth and anus polar. Here belong the common urchins, represented on our coasts by *Toxopneustes*,* *Strongylocentrotus*,* *Arbacia*,* *Cœlopleurus** (fig. 328).

Order III. Clypeastroidea.

Irregular flattened echinoids with central mouth and teeth; anus outside the periproct in the posterior interradius, sometimes marginal; five petaloid ambulacral areas. *Clypeaster* (tropical), *Echinarachnius** (sand dollar, fig. 333), *Mellita*,* with holes through the test.

Order IV. Spatangoidea.

Bilateral flattened forms more or less heart-shaped; mouth and anus excentric, no teeth; usually five petaloid ambulacral areas and four genital plates. From the forward position of the mouth it follows that only two ambulacral areas (bivium, p. 334) are upon the lower surface. Warmer seas. *Spatangus*,* *Echinocardium*, *Brissus*.

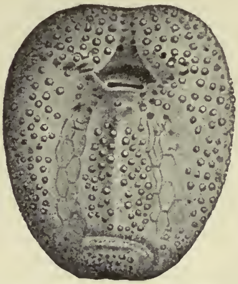


FIG. 334. Young *Spatangus purpureus* (after Agassiz), the spines removed, oral surface. In front, the slit-like mouth; behind, the anus. The bivium without tubercles.

Class V. Holothuroidea.

The sea cucumbers are most removed of any group from the typical echinoderm appearance. At the first glance the skin appears naked and the characteristic plates absent. Yet these are imbedded in the skin in the shape of plates, wheels, and anchors (fig. 335). The integment is tough, leathery, and muscular, with longitudinal and circular fibres. The saccular body gives these forms a worm-like appearance, strengthened by its elongation in the main axis, and with the mouth and anus at the poles. Unlike other echinoderms these move with the main axis parallel to the ground, a condition which, to a greater or less extent, leads to a replacement of radial by bilateral symmetry. One surface (trivium) becomes ventral, the bivium dorsal, and in many the trivial ambu-

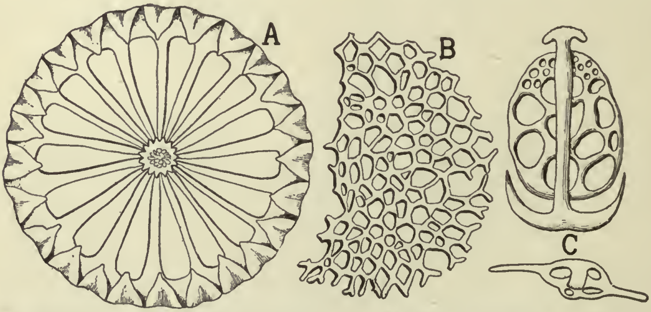


FIG. 335.—Dermal plates of Holothurians. *A*, *Myriotrochus rinkii*. (After Danielssen.) *B*, *Thyone briareus*; *C*, *Synapta girardii* (orig.).

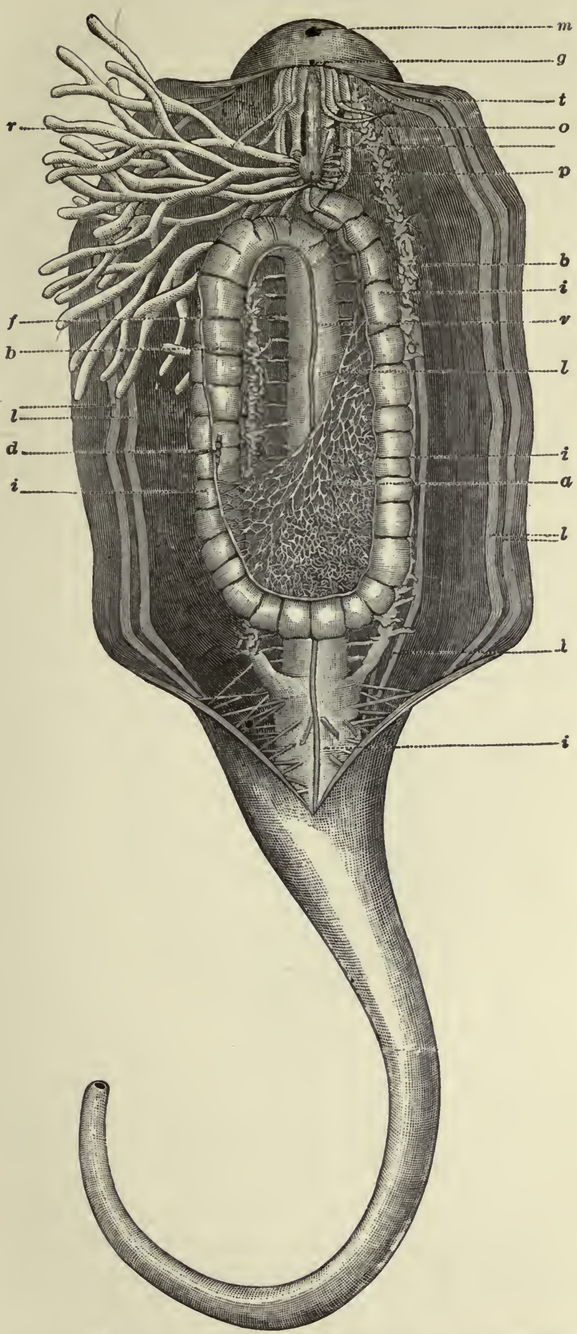


FIG. 336.—Anatomy of *Caudina arenata*. (After Kingsley.) *a*, anastomoses of dorsal blood-vessel; *b*, branchial tree; *d*, dorsal blood-vessel; *f*, mesenterial filaments; *g*, genital opening; *i*, alimentary canal; *l*, longitudinal muscles; *m*, mouth; *o*, genital duct; *p*, pharyngeal ring; *r*, gonads, cut away on right side; *t*, ampullæ of tentacles; *v*, ventral blood-vessel.

lacra alone are locomotor, those of the bivium being tactile or wholly absent.

In the body cavity (fig. 336) lies the alimentary canal, which (except in *Synapta*) is coiled in a uniform manner, although many minor convolutions may obscure this. It passes backwards in the median dorsal interradius, forward in the left ventral interradius, and then back in the right dorsal interradius to the anus. It is held in position by mesenteries (fig. 337), and near the anus by numerous muscular filaments. Into the terminal portion one or two branchial trees may empty. These are tubular sacs with small branched outgrowths which are filled with water. The similarity of these to the excretory organs of some Gephyræa (p. 317) was one ground for regarding those forms as intermediate between worms and echinoderms. They are to be regarded as respiratory, since they are periodically filled with fresh water. In many species 'Cuvierian organs' occur; these are morphologically specially modified portions of the branchial tree and are either connected with them or separately with the cloaca. Many zoologists regard them as defensive structures because of their sticky nature and because they can be cast out through the anus.

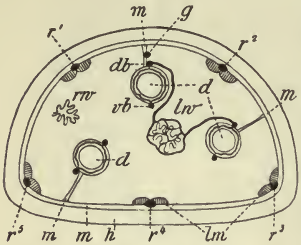


Fig. 337.—Transverse section of *Holothuria tubulosa.* (After Ludwig.) *d*, digestive tract; *db*, dorsal blood-vessel; *g*, gonad duct; *h*, skin; *lm*, longitudinal muscles; *lw*, left branchial tree; *m*, mesenteries; r', r^2, ambulacral complex of bivium (ambulacral vessel) and nerve; r^3-r^5, same of trivium; *rw*, right branchial tree.

The œsophagus is usually surrounded by a ring of five radial and five interradial plates which serve as points of attachment for the longitudinal muscles. Just behind it lie the ring canal, ring nerve, and the ring of the blood system, each giving off a radial branch which here runs inside the muscular sac of the body. From the beginning of the radial canals (rarely, as in *Synapta,* from the ring canal) tubes extend outward to form the extremely sensitive retractile tentacles which surround the mouth, and which either branch (Dendrochirotæ) or bear frilled shield-shaped extremities (Aspidochirotæ). A single Polian vesicle is usually present, and the stone canal (except in the Elasipoda) connects with the cœlom. Blood-vessels going from the vascular ring form rich anastomoses on the alimentary canal. Only a single gonad (or a pair of united gonads) occurs. This consists of numerous tubules which open usually interradially near the mouth.

The regenerative powers of these animals are of interest. In unfavorable conditions (hence in preserving the animals in alcohol without narcotization with chloral) they void the whole viscera and yet may live and reproduce the lost parts. In certain species are found a few parasites. One or two harbor a small fish (*Fierasfer*) in their cloaca and branchial trees. A parasitic snail, *Entoconcha mirabilis*, lives in one species of *Synapta*, and a mussel, *Entovalva mirabilis*, in another.

Order I. Actinopoda.

Radial canals present, sending branches to the tentacles and ambulacra when present. Divided into Pedata, with ambulacra, and Apoda, without. The PEDATA include the Holothuridæ with peltate tentacles. *Holothuria* * in warmer waters, one species furnishing the trepang of Chinese markets. The CUCUMARIIDÆ represented in our waters by *Cucumaria* * (*Pentacta*) with regular rows of ambulacra, *Thyone* * with them scattered, and *Psolus*,* scaly with a creeping disc. The deep-sea ELASIPODA belong to the Pedata. The APODA are represented by *Caudina* * (fig. 336) and *Molpadia*.*

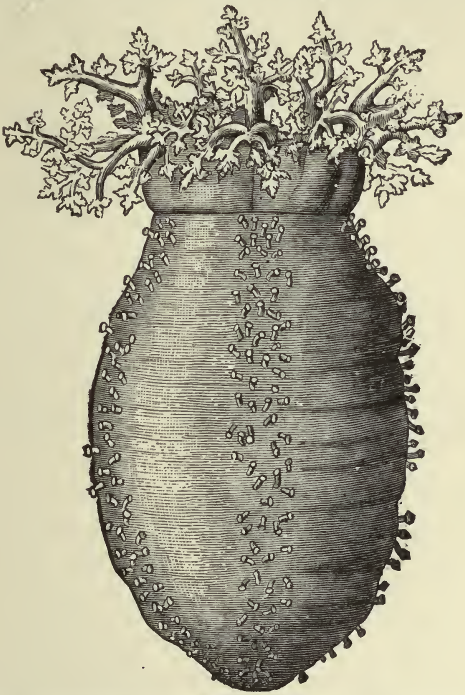


FIG. 338.—*Cucumaria frondosa*, sea cucumber. (From Emerton.)

Order II. Paractinopoda.

No radial canals nor ambulacra. Tentacular canals arising from ring canal. *Myriotrochus*,* *Synapta*,* *Oligotrochus* * (fig. 339).

Summary of Important Facts.

1. The ECHINODERMA share the radiate structure with the Cœlenterata, but differ from them (*a*) in the numerical basis of the symmetry (five); (*b*) in that, as embryology shows, they have descended from bilateral forms.

2. Farther characters are the existence of a cœlom, the ambulacral system, and the mesodermal spiny skeleton, which has given the name to the phylum.

3. The ambulacral system is locomotor and occurs nowhere else. It consists of a sieve-like plate, the madreporite (not always present), which passes water to the stone canal, and from this to the ring canal and the radial canals to fill the ampullæ and ambulacra. Lateral branches supply the tentacles and cause their extension.

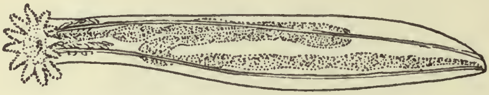


FIG 339.—*Oligotrochus vitreus.** (After Danielssen and Koren.)

4. Blood-vessels and nerve cords run in the same radii as the radial canals of the ambulacral system; stone canal, madreporite, ovoid gland, and genital ducts are interradial.

5. The Echinoderma are divided into five classes: (1) Asteroidea, (2) Ophiuroidea, (3) Crinoidea, (4) Echinoidea, and (5) Holothuroidea.

6. The ASTEROIDEA have a disc and (usually) five arms into which the gastric pouches and hepatic cæca extend. The ambulacral groove open.

7. The OPHIUROIDEA also have disc and arms, but the ambulacral groove is closed and the hepatic cæca absent.

8. The CRINOIDEA have a cup-shaped body bearing arms, usually branching, with pinnulæ, and a stalk, usually with cirri. They are either temporarily or permanently attached. The Crinoidea are subdivided into Eucrinoidea, Edrioasteroidea, Cystidea, and Blastoidea.

9. The ECHINOIDEA are usually spherical or oval, armored with calcareous plates which extend as meridional bands from peristome to periproct, five pairs of ambulacral and five of interambulacral.

10. The ambulacral plates end at the periproct with a single ocular plate; the interambulacral with a similar genital plate. The madreporite is fused with one of the genital plates.

11. The regular sea urchins have the anus in the centre of the periproct, the mouth in the peristome; the ambulacral areas are band-like.

12. The *Clypeastroidea* have a central mouth, the anus outside the periproct in the posterior interradius; the ambulacral areas petaloid.

13. The *Spatangoidea* are markedly bilateral, the mouth anterior, the anus posterior; ambulacral areas petaloid.

14. The HOLOTHUROIDEA are elongate and worm-like; the skeletal system greatly reduced; they are more or less bilaterally symmetrical and have usually a single gonad and two branchial trees. They are divided into Actinopoda, with radial canals, and Paractinopoda, without.

PHYLUM VI. MOLLUSCA.

At the first glance the molluscs, like the flatworms and leeches, give the impression of parenchymatous animals. A spacious cœlom is absent; what was formerly regarded as a body cavity is a system of sinuses surrounding the viscera and connected with the blood system, and is especially developed in the Acephala. More recently the view has gained ground that the molluscs have descended from cœlomate animals, and from forms in which, by encroachments of a connective tissue and muscular parenchyma, the cœlom has been reduced to the inconspicuous remnants of the pericardium and the lumen of the gonads.

Where the molluscan organization is well developed, as in the snails, four parts may be recognized in the body (fig. 340). The *visceral sac* forms the chief mass of the body; it is less rich in muscles than the rest because it is reduced to a thin peripheral layer by the alimentary canal, liver, nephridia, and gonads. In front it is continuous with the head, which, according to the group, is more or less marked off by a neck, and bears, besides the mouth, the tentacles and eyes, the most important sense organs. Below, the visceral sac passes into a muscular mass, usually used for locomotion, the *foot*. From the back extends the *pallium* or *mantle*, a dermal fold which envelops a goodly part of the body. The Acephala (fig. 340, *C*) have a double mantle, right and left, both halves springing from the dorsal line and extending down over the visceral sac and foot. The cephalopods (fig. 340, *A*) and the snails (fig. 340, *B*), on the other hand, have an unpaired mantle which arises from about the central part of the back and either extends down on all sides or, like a cowl, covers either the anterior or posterior parts of the body. The mantle is of importance in two ways: its outer surface is covered with epithelium which, like that of the adjacent surface, has the power of secreting shell, a thick cuticular layer of organic matter (conchiolin) largely impregnated with calcic carbonate. The inner surface of the mantle, together with the outer surface of the body, bounds a space, the mantle cavity, which, from its most important function, is also called the *branchial chamber*. Since most molluscs are aquatic, special vascular processes of the body, the gills or branchiæ, lie in this space; in the terrestrial forms its walls serve as lungs and thus are respiratory.

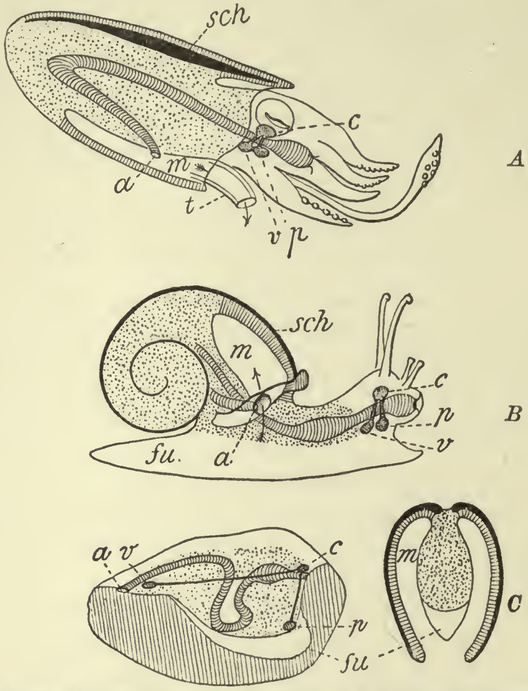


Fig. 340.—Diagrams of three molluscan classes. *A*, a cephalopod (*Sepia*); *B*, a gasteropod (*Helix*); *C*, an acephal (*Anodonta*). *a*, anus; *c*, cerebral ganglion; *fu*, foot; *m*, mantle chamber; *sch*, shell; *t*, siphon; *v*, visceral ganglion. Visceral sac dotted; mantle lined, shell black.

From the foregoing it will be seen that the character of the mantle must exert an influence on the shape of the shell and on the respiratory organs. Paired mantle folds necessitate two valves, right and left, to the shell; a right and left branchial chamber, and right and left gills. With an unpaired mantle the shell is always unpaired, while the gills may retain their primitive paired condition.

The gills in the mantle cavity are called *ctenidia*, from their resemblance to combs with two rows of teeth. Each consists of an axial portion (back of the comb), containing the chief blood-vessels and two rows of branchial leaves. The whole is united to the wall of the branchial cavity by the axis (fig. 385). In many aquatic forms the ctenidia are lacking, and then the respiration is either diffuse by the skin or by accessory gills which by structure (usually outside the mantle cavity) are distinguished from the ctenidia.

Those parts of the surface of the mollusc which are not covered by the shell have a columnar epithelium which is frequently ciliated and which contains unicellular mucus glands, especially abundant on the edge of the mantle. These give these animals the soft slippery skin which is implied in the name Mollusca (*mollis*, soft). Many-celled glands, like the byssus gland of the Acephala, the pedal gland of many snails, occur.

Although the existence of head, foot, and mantle is very characteristic of the molluscs, they are not always present. In the Acephala there is no distinct head region; many gasteropods lack the mantle and hence the shell; in the Cephalopoda the foot is converted into other appendages, the siphon and arms. These modifications are to be explained by degeneration and evolution. In the nervous system are also some highly characteristic features. As a rule it consists of three pairs of ganglia associated with important sense organs and connected by nerve cords. One pair lies dorsal to the œsophagus and corresponds to the supraœsophageal ganglion of the worms; it is the brain (cerebrum) and supplies

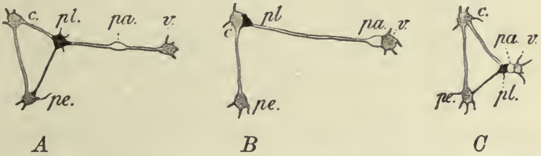


FIG. 341.—Nervous systems of Molluscs. *A*, most gasteropods; *B*, acephals; *C*, cephalopods and pulmonates. *c*, cerebral; *pa*, parietal, *pe*, pedal, *pl*, pleural, and *v*, visceral ganglia.

the tentacles and eyes. A second pair lies ventral to the alimentary tract on the front part of the muscle mass of the foot; these are the pedal ganglia which are connected with the otocysts. The third pair, the visceral ganglia, are also ventral, and near them are the third sense organs, which are widely distributeed through the Mollusca, and which from position and structure are regarded as organs of smell (*osphradia*). They are thickened patches of ciliated epithelia extending into the mantle cavity. Pedal and visceral ganglia are united to the cerebrum by nerve cords, the cerebropedal and cerebrovisceral connectives respectively. Accordingly as these connectives are long or short the ganglia are wide apart or united into a nerve mass around the œsophagus.

Primitive Mollusca (Amphineura) have a simpler condition. The cerebral ganglia lie dorsal to the œsophagus and are united by a cord around the œsophagus (fig. 344). From it are given off two pairs of lateral nerve tracts, the ventral or pedal cords, and lateral or pleural cords, the latter united by a loop dorsal to the anus. By a concentration of ganglion cells the pedal cords give rise to the pedal ganglia, and similarly the pleural cords form three pairs of ganglia, the pleural and the parietal, as well as the visceral already mentioned, of the cerebrovisceral cord (fig. 341, *A*). The pleural ganglia are connected with the pedal by nerve cords; the parietal innérvates the osphradium. When farther concentration takes place the pleural may unite with the cerebral, and the parietal with the visceral (fig. 341, *B*), or both may fuse with the visceral (*C*). In the latter case the visceral ganglion (in the wider sense) is associated with the pedal by the pleuropedal connective; while in the other the connective is apparently absent because fused with the cerebropedal. Although the otocyst receives its nerve from the pedal ganglion, the centre of innervation lies in the cerebrum.

The heart, which lies dorsally, consists of auricles and ventricles. The ventricle is always unpaired, but there are two auricles where two gills exist from which the blood flows to the heart, but with the loss of one gill one auricle may disappear. Distinct arteries and veins occur; capillaries are found only in the Cephalopoda, while in the lower molluscs, and especially in the Acephala, the smaller arteries open into lacunar spaces which were formerly regarded as the body cavity. A completely closed vascular system does not exist even in the Cephalopoda.

The heart is enclosed in a spacious sac or pericardium, which, with few exceptions, is connected with the nephridia by a ciliated canal, and in many molluscs (Cephalopoda and some Acephala) is also related to the gonads. These facts support the view, already mentioned, that the pericardium and the lumen of the gonads are the remnants of the cœlom; for here, as in the annelids, the nephridia open by ciliated nephrostomes into the cœlom, and the sexual cells arise either from the cœlomic walls or from sacs cut off from them. Even more important for this view would be confirmation of the disputed statement that in *Paludina vivipara* the cœlom (enterocœle) arises as diverticula from the archenteron.

Nephridia and sexual organs are primitively paired, but frequently are single by the degeneration of the structures of one side. The animals are either hermaphroditic or diœcious, but the gonads are always very large. Even more room in the visceral sac is demanded by the digestive tract in which œsophagus, stomach, a coiled intestine, a voluminous liver, and frequently salivary glands may be recognized. The radula or lingual ribbon is also a characteristic organ, and its absence from the Acephala is probably to be explained by degeneration. It is a plate or band armed with teeth which lies on the floor of the pharynx on a ventral ridge, the tongue, and is used for the communication of food (figs. 366, 367).

Reproduction is exclusively sexual; budding, fission, or parthenogenesis have not yet been observed. The eggs, united in large numbers, are usually enveloped in jelly and are either rich in deutoplasm or are enveloped in a nourishing albumen. A few molluscs (*e.g.*, *Paludina vivipara*) are viviparous. A metamorphosis is of wide occurrence. In such cases a 'veliger' larva escapes from the egg (fig. 342); in this can be recognized head, foot, and mantle, even in those cases where one or the other of these is lacking in the adult. This shows that the absence of

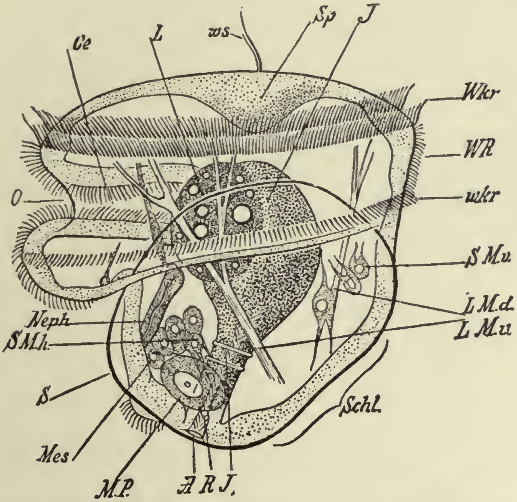


FIG. 342.—Veliger larva (trochophore) of *Teredo navalis*. (From Hatschek.) *A*, anus; *J*, stomach; J_1, intestine; *L*, liver; *LM.d*, *LM.v*, dorsal and ventral longitudinal muscles; *Mes*, primitive mesoderm cells; *MP*, teloblast; *Neph*, protonephros; *O*, mouth; *Oe*, œsophagus; *R*, rectum; *S*, shell; *Schl*, hinge; *SM.h*, *SM.v*, posterior and anterior adductors; *Sp*, apical plate; *Wkr*, *wkr*, pre- and postoral ciliated bands; *ws*, cilia of apical plate.

mantle, shell, or head, which occur in large groups of molluscs, is not a primitive condition, but can only be explained by degeneration. The name veliger arises from the velum, a strong circle of cilia, which surrounds a frontal or velar field in front of the mouth, and which serves as a locomotor organ for the larva. In some cases (fig. 343 *B*) it is lobed like the trochus of a Rotifer.

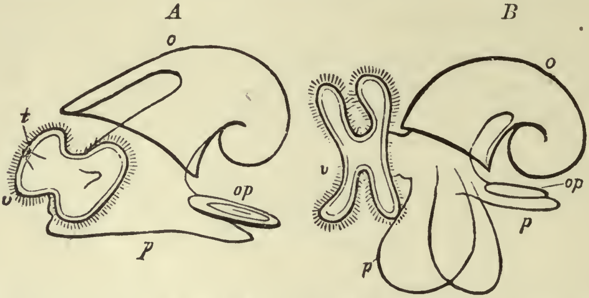


FIG. 343.—Veliger stages, *A*, of a snail; *B*, of a Pteropod. (From Gegenbaur.) *o*, shell; *op*, operculum; *p*, foot; *t*, tentacle; *v*, velum.

The veliger recalls the annelid trochophore and serves for the distribution of the species; it is therefore of great importance for animals which, like most molluscs, are sedentary or slow-moving. In cases without metamorphosis (Cephalopoda, Pulmonata, etc.) the veliger stage is frequently indicated during embryonic development by a ridge of cells surrounding a preoral velar field.

Class I. Amphineura.

These forms, some of which appear in the Silurian, are clearly the most primitive of molluscs, and are distinguished by a marked bilateral symmetry. The nervous system already described (p. 354) consists of pleural and pedal cords with scattered ganglion cells and no ganglia, these cords being connected by numerous commissures (fig. 344, *B*).

Sub Class I. Placophora (*Chitonidæ*).

The chitons were formerly included among the gasteropods because of the presence of a creeping foot and a radula. They are at a glance distinguished from them by the rudimentary condition of the head and the shell. This last is unique among molluscs; it consists of eight transverse plates overlapping like shingles, which allows the animal to roll itself into a ball. The edge of the mantle extends beyond the shell and is covered with spines, while in the mantle cavity beneath are, right and left, a series of ctenidia. Nerves enter the shell and end with noticeable sense organs (æsthetes and, in some, eyes, fig. 345). The symmetry of the body is also expressed in the viscera. The anus is medial, and right and left of it are the openings of the nephridia and sexual organs. The sexes are separate, the gonads unpaired, while corresponding to the paired arrangement of the gills there are two auricles to the heart.

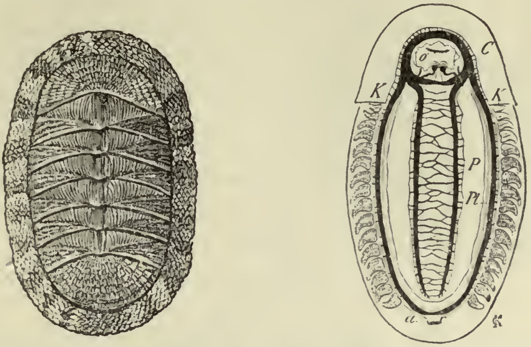


FIG. 344.—*Chiton squamosus*, dorsal view. (After Haller.) *A*, the entire animal; *B*, after removal of shell and viscera. *a*, anus; *C*, brain; *K*, ctenidia; *o*, mouth; *P*, pedal nerve cord; *pl*, pleurovisceral nerve cord.

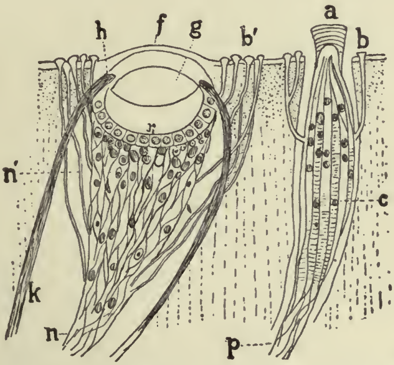


FIG. 345.—Eye and æsthetes of *Acanthopleura spiniger*. (After Moseley.) *a*, macræsthete; *b*, micræsthete; *f*, calcareous cornea; *g*, lens; *h*, iris; *k*, pigmented capsule; *n*, *p*, nerves; *r*, retina.

The Chitons are represented on our northeastern coast by several small species (*Trachydermon*,* *Amicula* *); farther south and on the Pacific shores are larger species (*Cryptochiton* *).

Sub Class II. Solenogastres (*Aplacophora*).

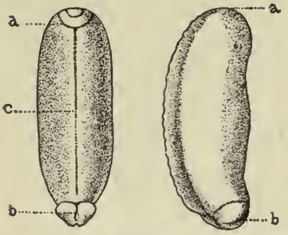


FIG. 346. — *Neomenia carinata*, ventral and side views. (After Tulberg.) *a*, anterior; *b*, posterior; *c*, ventral groove.

Worm-like forms without shell; the foot rudimentary and at the bottom of a ventral groove. The radula is also reduced; in *Chætoderma* it bears but a single tooth. The gills are either small or wanting. The usually hermaphrodite animals have the gonads emptying into an unpaired chamber (pericardium?) and thence to the exterior by the paired nephridia. *Chætoderma* in New England; *Neomenia*, *Dondersia*.

Class II. Acephala (Lamellibranchiata, Pelecypoda).

These have, among the molluscs, the least powers of locomotion. Some are fixed, the majority burrow slowly through sand or mud; only a few spring by means of the foot or swim by opening or closing the shells. Hence it is that they need more protection than other species, and this is afforded by the strong shells in which the body can usually be completely enclosed. This shell recalls that of the brachiopod in that it consists of two halves or valves, but these valves are right and left rather than dorsal and ventral, and hence are usually symmetrical in shape. Only when the animal rests permanently on the right or left side is this symmetry lost, and then the symmetry of the soft parts is affected.

The two lobes of the mantle which secrete the shell on their outer surface arise from the back of the animal and grow downwards, forwards, and backwards, so that they envelop the whole (fig. 352). Hence the oldest and the most thickened part of the shell, the umbo, occurs near the back (fig. 347). Around this the *lines of growth* are arranged concentrically, lines which show how, by gradual growth of the mantle, the shell has increased in size. On the back the valves approach each other, and in the majority are movably connected by a hinge, which consists of projections ('teeth') in one valve fitting into depressions in the other. In the Brachiopoda the valves are opened by appropriate muscles; in the Acephala by an elastic hinge ligament usually placed dorsal to and behind the hinge. The shell is closed by adductor muscles which extend through the body from shell to shell, leaving their impressions or scars on the inner surface (fig. 347).

Usually there occur an anterior and a posterior adductor equally well developed (Dimyaria); less frequently the anterior is rudimentary (Heteromyaria) or entirely disappears (Monomyaria).

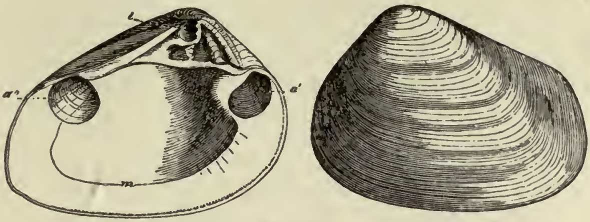


FIG. 347.

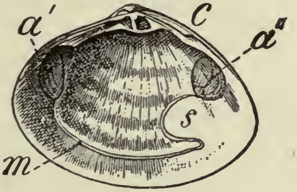


FIG. 348.

FIG. 347.—Left valve of *Crassatella plumbea*, inner and outer surfaces. (From Zittel.) The outer surface showing lines of growth; no pallial sinus.
FIG. 348.—Right valve of *Mactra stultorum*, with pallial sinus. (From Ludwig-Leunis.) Letters for both figures: *a'*, anterior; *a''*, posterior adductor scar; *e*, hinge; *l*, internal ligamental groove; *m*, pallial line; *s*, pallial sinus.

When the muscles are relaxed (as always occurs at death) the elastic ligament opens the valves.

The heterodont hinge is the typical form (fig. 348); each valve bears a group of teeth near the umbo, those of the left alternating with those of the right. Besides these '*cardinal teeth*' there are in front and behind '*lateral teeth*,' often produced into ridges. The ligament lies behind the hinge and is usually visible from the outside (external ligament), but is occasionally transferred to the interior (internal ligament, fig. 347). The so-called schizodont and desmodont hinges are modifications of the heterodont. Then there are Acephala of apparently primitive character which either lack the hinge (dysodont), or have one composed of numerous teeth in a series symmetrical to the umbo (taxodont), or of two strong teeth likewise symmetrical to the umbo (isodont). In these cases the ligament is developed in front of as well as behind the umbo, and may be either external or internal.

Since the secretion of shell takes place most rapidly at the edge of the mantle, both are closely united, the union being strengthened by small muscles. So the edge of the shell has a different appearance from the rest, this part being marked off by a pallial line parallel to the margin (fig. 347). In many species, the Sinupalliata, the line at the hinder end makes a large bay (*pallial sinus*) (fig. 348, *s*). Since the mantle folds are membranes with free margins, it follows that when the shell is closed these edges are pressed together, which would prevent the free entrance and exit of water. To accommodate this each mantle has its margin excavated at the posterior end, so that when brought together two openings, an upper and a lower, result (fig. 349, *C*). The lower of these is the branchial opening by which fresh water passes into the mantle (branchial) chamber; it flows out after passing over the gills, along with the fæces, through the upper or cloacal opening. In many bivalves the free edges of the mantle grow together, leaving three openings, one for the protrusion of the foot, the others the two just described, which are now called the incurrent (branchial) and excurrent (cloacal) siphons (fig. 349, *B*). By further development the margins of these openings are drawn out

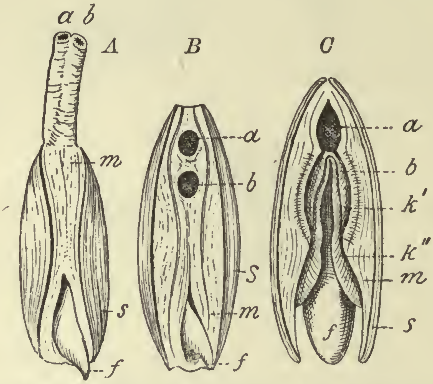


FIG. 349.—Ventral views of siphonate and asiphonate acephals. *A*, *Anodonta cygnea*; *B*, *Isocardia cor*; *C*, *Lutraria elliptica*. *a*, anal siphon; *b*, branchial siphon; *f*, foot; *k'*, outer, *k''*, inner gill lamella; *m*, mantle; *s*, shell.

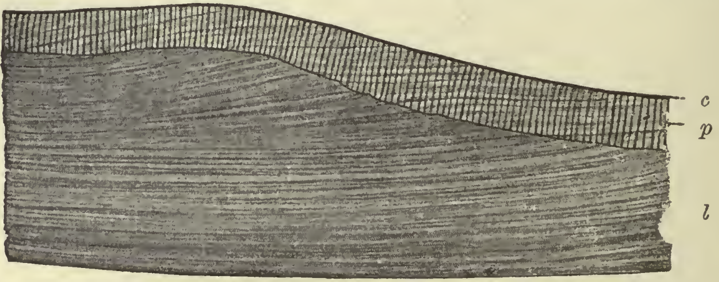


FIG. 350.—Section of shell of *Anodonta*. *c*, cuticula; *p*, prismatic layer; *l*, nacreous layer.

into two long conjoined tubes (fig. 349, *A*), which for their retraction need special muscles, which are attached to the valves and thus cause the pallial sinus referred to above (fig. 348).

In the shell three layers may be distinguished (fig. 350): on the outside a thin organic cuticula and below two layers largely of calcic carbonate. In many these two layers are distinguished as the prismatic layer and the nacreous layer, the first consisting of closely packed prisms; the nacreous layer of thin lamellæ generally parallel to the surface. These by their free edges produce diffraction spectra and so the iridescent appearance of the shell; the finer the lines thus formed the more beautiful the play of colors. This is especially noticeable in the mother-of-pearl shells *Meleagrina* and *Margaritina margaritifera*. When foreign substances get between mantle and shell they stimulate a greater secretion of nacreous substance and become surrounded by layers of it. In this way pearls are formed.

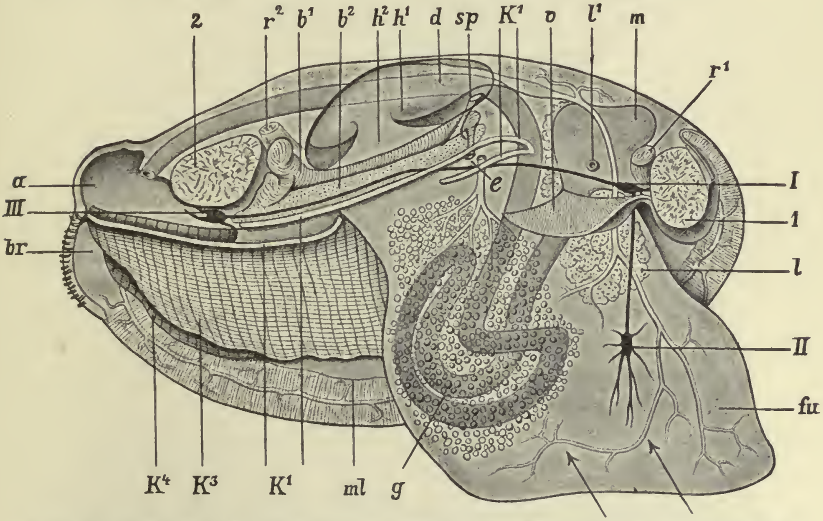


FIG. 351.—Anatomy of *Anodonta*, the mantle, gill, and liver of the right side removed, the pericardium opened. *1*, *2*, anterior and posterior adductors; *I*, *II*, *III*, cerebral, pedal, and visceral ganglia; *a*, anus; b^1, b^2, upper and lower limbs of organs of Bojanus; *br*, branchial siphon; *d*, intestine; *e*, nephridial opening; *fu*, foot; *g*, gonad; h^1, h^2, ventricle and auricle of heart; k', insertion of both lamellæ of right gill; k^3, k^4, inner and outer lamellæ of left gill; *l*, left liver; l', its opening in *m*, stomach; *ml*, pallial line; r^1, anterior, r^2, posterior retractor muscle: *sp*, nephrostome; *v*, labial palpus. The arrows show the planes of section of fig. 352.

The gills lie between the mantle and the body and from their lamellar character have given rise to the name Lamellibranchiata (figs. 351, 352). Two gill-leaves occur on either side, although occasionally the outer or both may degenerate. Frequently the gills of the two sides unite behind the body and produce a partition which separates the mantle cavity into a small dorsal cloacal chamber and the larger lower respiratory cavity. Into the cloaca empty the anus and the water which has passed over the gills; it opens to the exterior through the excurrent siphon. The incurrent siphon leads into the branchial chamber. In front of the gills are two more pairs of leaf-like lobes, the *labial palpi,* between which is the mouth.

The gills are variously developed. The Nuculidæ—the most primitive of living Acephala—have true ctenidia consisting of an axis grown to the body and an inner and an outer row of gill leaves (fig. 355). From this the filibranch type is easily derived. The gill leaves grow out into long filaments, each bent on itself so that it presents two limbs, a descending and an ascending. These branchial threads are so matted together that they give the impression of a continuous leaf. In the true lamellar gill the threads of the filibranch grow together at intervals, leaving openings, the gill slits. Since there is an ascending and a descending limb, it follows that each gill consists of an inner and an outer leaf (fig. 352), leaving a space between into which the gill slits open. This internal space in some serves to contain the young.

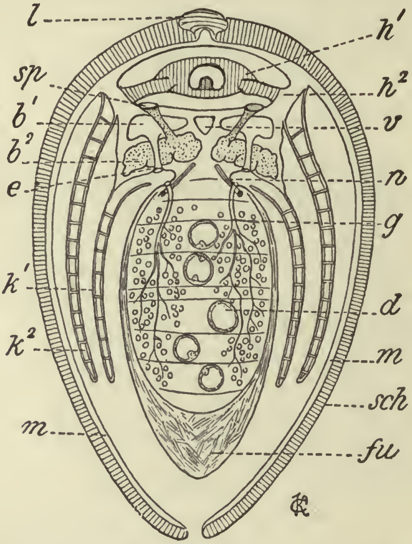


FIG. 352.—Projection of sections shown by the arrows in fig. 351. b^1, b^2, upper and lower limbs of nephridium (organ of Bojanus); *d*, intestine; *e*, nephridiopore; *fu*, foot; *g*, gonad; h^1, ventricle surrounding the intestine; h^2, auricle; k^1, k^2, inner and outer gill lamellæ; *l*, hinge ligament; *m*, mantle; *n*, cerebro-visceral commissure; *sp*, nephrostome; *v*, venous sinus.

The complete enclosure of the body in the mantle folds has led to a degeneration of the head and its normal appendages

(Acephala). Hence there are only two divisions in the body, dorsally the visceral sac and ventrally the foot. The foot, degenerate in many, has a broad sole only in *Pectunculus* and the Nuculidæ; usually it is hatchet-shaped (Pelecypoda), that is, compressed with a rounded ventral margin. It may be enormously expanded and contracted again. This expansion is often explained by the taking of water into the blood, but now it is generally accepted that it is accomplished by forcing blood from other regions into it. While the foot by this extensibility can serve as a locomotor organ, it also functions in many as an organ of attachment. Inside is a large byssus gland which can secrete silky threads, the byssus (fig. 353), one end of which is fastened to foreign objects by means of a finger-like process of the foot, while the other end remains in connection with the foot. Molluscs which have a byssal gland are found anchored by a thick bunch of byssal threads to stones, etc.

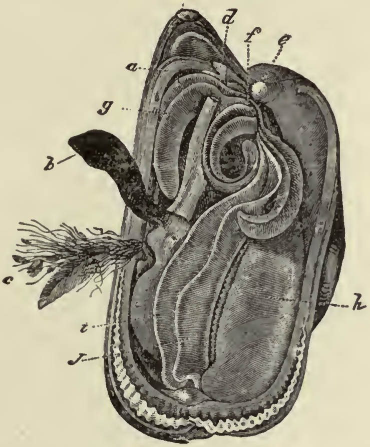


Fig. 353.—*Mytilus edulis**. (After Blanchard.) *a*, edge of mantle; *b*, spinning finger of foot; *c*, byssus; *d*, *e*, retractors of foot; *f*, mouth; *g*, labial palpi; *h*, mantle; *i*, *j*, inner and outer gills.

The heart, surrounded by a pericardium, usually occupies the most dorsal part of the visceral sac. It consists of a ventricle and a pair of auricles (figs. 351, 352, h^1, h^2). The auricles receive the blood direct from the gills; the ventricle forces it out through anterior and posterior aortæ (fig. 351), the latter lacking in many species.

The excretory organs (organs of Bojanus) lie immediately below the pericardium. The organs of the two sides touch in the middle line. Each consists of a dorsal smooth-walled chamber and a lower portion traversed by threads, both connected behind but separated elsewhere by a thin partition. The lower chamber is connected in front with the pericardium by a ciliated canal, the nephrostome, while the upper opens to the outside by a short canal, the ureter, the external opening being in the region of the inner cavity of the inner gill. In this way a connexion is established from the pericardium to the exterior, the apparatus being apparently a true nephridium. In many it serves also as genital duct, but usually the genital and reproductive ducts are separate. The animals are usually diœcious, the gonads being acinose glands.

The digestive tract (fig. 351) begins with a short œsophagus, widens out to a large stomach from which a slender intestine leads, with many convolutions, to the anus. In the majority of Acephals the terminal portion enters the pericardium in front and below, passes through the ventricle and out through the upper posterior wall of the pericardium. In its course the alimentary tract is enveloped by the gonads and the voluminous liver, the secretion of the latter emptying by two ducts into the stomach. Usually the stomach has a blind sac, in which lies the 'crystalline style,' a rod-like structure of uncertain significance.

The three typical molluscan ganglia (p. 353) are uncommonly wide apart. The two brain ganglia (cerebropleural ganglia) lie either side of the mouth at the base of the labial palpi and ventral to the anterior adductor. They are very small, since cephalic sense organs are lacking, and are united by a transverse supraœsophageal commissure. The posterior ganglia, composed of the united parietal and pedal ganglia, lie near the anus ventral to the posterior adductor. The pedal ganglia, rather far forward in the muscles of the foot, are closely approximate. Of the higher sense organs only the otocysts near the foot are constant. The labial palpi are also highly sensory, while two small osphradia occur at the basis of the gills. When eyes occur they are, as in the scallops (Pectinidæ), arranged in a row like pearls on the margin of the mantle. Small tentacles with sensory powers may occur both on the margin of the mantle and on the tip of the siphon.

Veligers (fig. 342) are very common in development. When this stage is lacking the history may contain a metamorphosis as in the fresh-water *Anodonta.* The young which grow in the maternal gills are known as Glochidia, which are distinguished from the adult by a byssus thread, by only a single adductor, and by a hook or tooth on the free margin of the shell (fig. 354). After escape from the gills they swim about by opening and closing the shells, and by means of the hooks attach themselves to passing fish. They produce an ulcer in the skin of the fish in which they grow, and by renewal of the shell and the adductor muscles attain the definitive condition. After this metamorphosis they fall to the bottom, to live henceforth half buried in the mud.

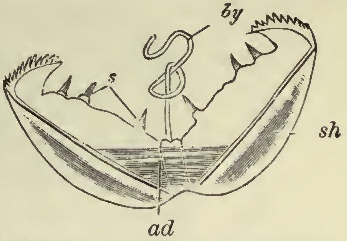


FIG. 354.—Glochidium of *Anodonta*. (From Balfour.) *ad*, adductor; *by*, byssus; *s*, sense hairs; *sh*, shell.

Structure of gills, hinge, edge of mantle, and adductor muscles have been used as basis of classification, the usual divisions being founded on characters derived from only one of these organs.

Order I. Protochonchiæ.

The primitive character of these forms is shown by the structure of the gills, which are either ctenidia (Protobranchiata) or filamentary (Filibranchiata), yet here and there, as in the scallops and oysters (Pseudolamellibranchiata), the fusion of gill filaments is already begun. Hinge and ligament are symmetrical with regard to the umbo, or vary little from symmetry. The hinge may be lacking, and the ligament is wholly or in part internal. The mantle edges are free, and rarely is there the first trace of fusion.

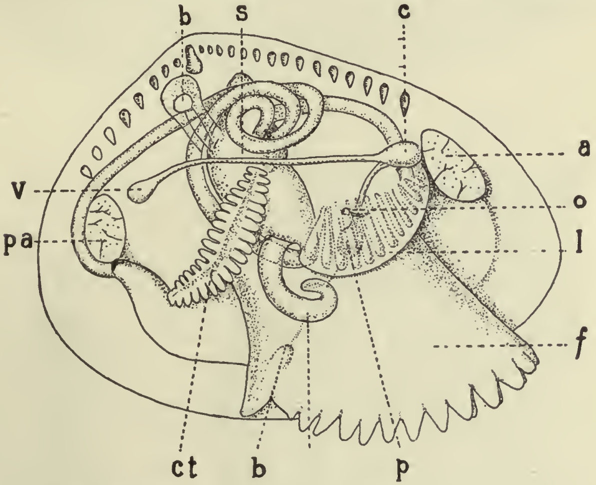


FIG. 355.—Anatomy of *Nucula*. (After Drew.) *aa*, anterior adductor; *b*, byssal gland; *c*, cerebral ganglion; *ct*, ctenidium; *f*, foot; *h*, heart; *l*, labial palpus; *o*, otocyst; *p*, pedal ganglion; *pa*, posterior adductor; *s*, stomach; *t*, appendage of palpus; *v*, visceral ganglion.

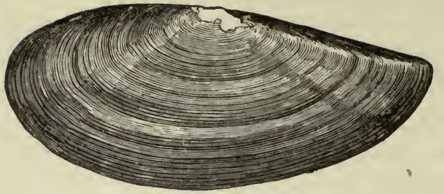


FIG. 356.—*Yoldia limatula.** (From Binney-Gould.)

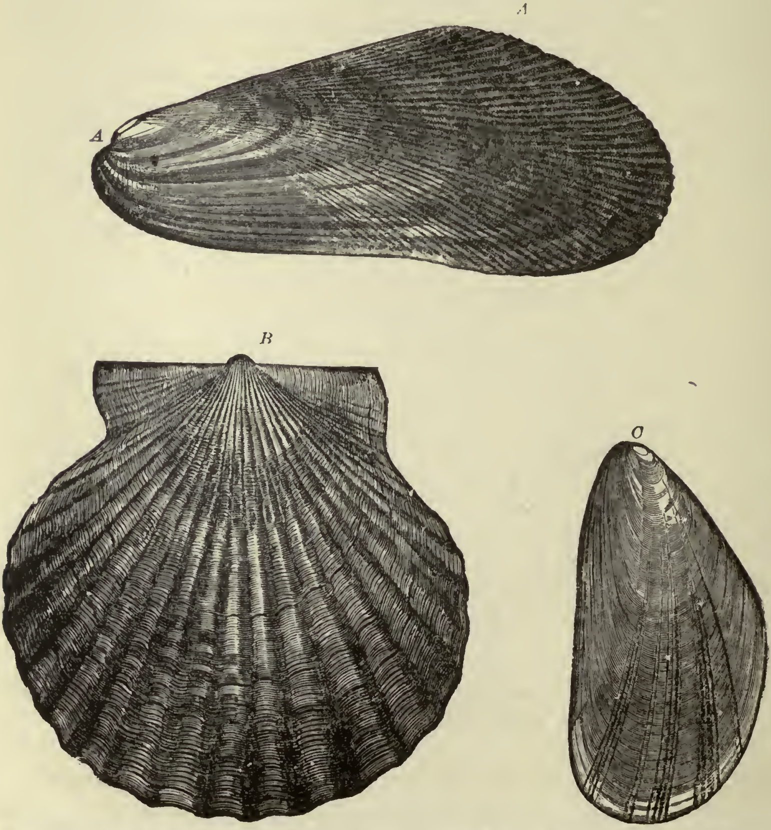


FIG. 357.—*A*, *Modiola plicatula**; *B. Pecten irradians**; *C*, *Mytilus edulis.** (From Binney-Gould.)

Sub Order I. DIMYARIA. Two equally developed adductors. The taxodont NUCULIDÆ have ctenidia, a broad foot, pleural and cerebral ganglia separate, and gonads emptying through the nephridia, all points which show them extremely primitive. *Nucula*,* *Leda*,* *Yoldia*.* The ARCIDÆ are also taxadont, but filibranch. *Scapharca*,* *Argina*.* SOLEMYIDÆ.

Sub Order II. ANISOMYARIA. Anterior adductor rudimentary (Heteromyaria) or wanting (Monomyaria). With the exception of the isodont SPONDYLIDÆ, all the families lack a hinge (dysodont). To the Heteromyaria belong the MYLILIDÆ, or mussels, with strong byssus and shells pointed anteriorly. *Modiola*,* *Pinna*,* *Mytilus edulis*, abundant on our mud flats; eaten in Europe, but occasionally poisonous. *Dreissenia polymorpha*, a brackish and fresh-water species, has spread from the Caspian through central Europe. *Lithodomus** bores into stone. The AVICULIDÆ of warm seas have wing-like projections either side of the umbo. The pearl oysters of the East and West Indies (*Meleagrina*) belong here. The OSTRÆIDÆ and the PECTINIDÆ are monomyarian. The Ostræidæ, or oysters, usually become attached by the right valve. Our American *Ostræa virginiana* differs from the European species in having the sexes separate. The Pectinidæ, or scallops, are free-swimming and are well known for their highly developed green eyes on the edge of the mantle.

Order II. Heteroconchiæ.

Gills always lamellar, their outer surface frequently plaited. Hinge—in rare cases (*Anodonta*) lost by degeneration—is heterodont or modified from a heterodont condition. The mantle edges but rarely free in their whole extent; siphons usually present, but in some so small (Integripalliata) as to cause no sinus in the pallial line; in others (Sinupalliata) large, the pallial line having a marked sinus. Anterior and posterior adductors equally developed.

Sub Order I. INTEGRIPALLIATA. The UNIONIDÆ (Naiadæ) include the fresh-water mussels, of which hundreds of species occur in the Mississippi basin, some of which are markedly iridescent and afford material for pearl buttons. In some pearls of value are occasionally found. *Unio*,* *Anodonta*.* The tropical TRIDACNIDÆ, with small siphons, includes the largest Acephala, *Tridacna gigas*, the shell of which may be four feet long and weigh three hundred pounds. The heart shells (CARDIIDÆ—

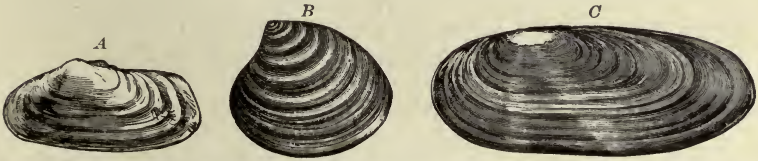


FIG. 358.—*A*, *Saxicava arctica*; *B*, *Astarte sulcata*; *C*. *Siliqua costata*. (From Binney-Gould.)

*Cardium**, *Serripes**) and ASTARTIDÆ, marine, and the fresh-water CYCLADIDÆ (*Cyclas*, *Pisidium**), about the size of peas, belong here, as probably do the extinct RUDISTIDÆ of the cretaceous.

Sub Order II. SINUPALLIATA. The VENERIDÆ with swollen shells, represented by the quahog, *Venus mercenaria* on our east coast and by brightly colored species in the tropics; the MACTRIDÆ or hen clams, and the flattened delicate TELLINIDÆ (*Tellina**, *Macoma**), have short siphons. In others the siphons are so large that they cannot be entirely retracted within the shell. This is the case in the MYIDÆ, represented in all northern seas by the long clam, *Mya arenaria*, and in the razor clams (SOLENIDÆ; *Solen Ensatella**). The allied SAXICAVIDÆ have burrowing species. These forms connect with others in which the united siphons far exceed the rest of the body in length, giving the animal a worm-like appearance (fig. 359). Since the valves do not cover the whole shell, they are supplemented by accessory shells, or the worm-like body secretes a tube in which the rudimentary valves are imbedded (fig. 360). The PHOLADIDÆ, some of which are phosphorescent, burrow in wood, clay, or stone. The shell is well developed. In the ship worms (TEREDIDÆ) the shells, on the other hand, are small, while in some species the burrows made by these animals in wood are lined by calcareous deposits. The several species of *Teredo** by their boring habits do much damage to wood in the sea, especially in the tropics. The GASTROCHÆNIDÆ also form tubular shells, the valves being imbedded in the tube (fig. 360); at the smaller anterior end the tube is open, but the other end is closed by a perforated plate, giving these animals the name of 'sprinkling-pot' shells.

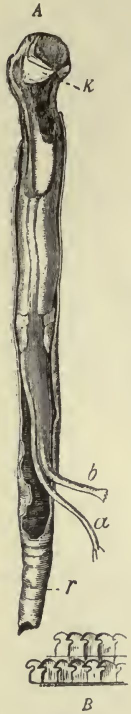


FIG. 359.—*Teredo navalis*, ship worm in its tube, the siphons (*a*, anal; *b*, branchial) drawn out of the tube (*r*); *k*, shell. *B*, teeth of the shell enlarged.

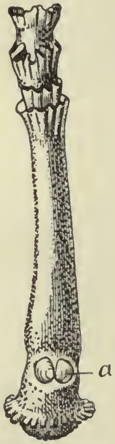


FIG. 360.—Tube of *Aspergillum vaginiferum*. (From Ludwig-Leunis.) *a*, shell.

Lastly, there should be mentioned the little-known Septibranchiata, in which the gills have the shape of a septum perforated by gill slits separating the branchial and cloacal chambers. *Silenia*, *Cuspidaria*.

Class III. Scaphopoda (Solenoconchæ).

The tooth shells are primitive forms which have some resemblances to the Acephala in the paired liver and nephridia and in structure of the nervous system (with the exception that a buccal ganglion is present and the pleural ganglia are distinct from the cerebral). In some points they are primitive (persistence of jaws and radula), but in others they are considerably modified. They lack gills, have unpaired diœcious gonads, rudimentary heart (no auricle), and have two bunches of thread-like tentacles either side of the mouth. The mantle lobes, which are paired in the larva, unite below, forming a sac open at either end, and this secretes a shell shaped like the tusk of an elephant, from the larger end of which protrudes the long three-lobed foot used for boring in the sand. *Dentalium* (fig. 361), *Entalis**.

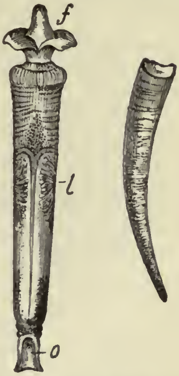


Fig. 361.—*Dentalium elephantinum*, tooth shell; left the animal, right the shell *f*, foot; *l*, liver region; *o*, hinder opening of mantle.

Class IV. Gasteropoda.

Although more highly organized than the Acephala, the snails are in some respects more primitive. The regions of the body—foot, visceral sac, head, and mantle—occur in all orders, although in each one or more forms may occur in which one or another part is lost.

As a rule the foot is flattened ventrally to a creeping sole. In it may be distinguished anterior and posterior processes, the *propodium* and *metapodium*, a sharp lateral margin, the *parapodium*, and, above these, appendages or ridges, the *epipodia*. Inside the foot is usually a pedal gland.

The head bears (1) the tentacles, a pair of muscular lobes or hollow retractile processes; (2) a pair of primitive vesicular eyes, which usually lie at the basis of the tentacles, but may rise even to their tips. In many snails the eyes are on special stalks which, as in the stylommatophorous Pulmonata, form a second pair of tentacles. The protrusion of the tentacles is caused by an inflow of blood, their retraction by muscles attached to the tip which draw them in like a finger of a glove.

The mantle begins on the back and extends thence forward over the body to near the beginning of the head. It covers the mantle cavity, a spacious chamber, which in the water-breathing Prosobranchiata, etc., contains the gills (ctenidia) and opens outward by a large aperture under the margin of the mantle. The edge of the mantle may be produced into a long groove-like siphon, conveying water to and from the branchial chamber, which is of importance in determining the shape of the shell. When, by degeneration of the gill, the animals become air-breathing, the mantle cavity becomes a lung, and the opening, by growth of the mantle edges to the body, becomes a small spiraculum, closed by muscles.

The visceral sac, by the great development of the gonads and liver, becomes very large. Since growth downwards is prevented by the muscular foot, the organs press towards the back, carrying before them the dorsal wall at the origin of the mantle folds, the line of least resistance. Some organs, like nephridia and heart, may be pressed into the mantle cavity. When the visceral sac, as often occurs, becomes enormous, it does not stand directly upwards, but coils from left to right in a spiral. The older the animal the more the spiral coils and the larger the last or body whorl. The visceral spiral therefore begins at the tip with narrow whorls which increase in size with approach to the rest of the body.

From the foregoing the shape of the shell is easily understood. As a secretion of the mantle it takes the form which the mantle assumes under the influence of the visceral sac. With slight development of the visceral sac it forms a flattened cone (fig. 362, *A*), or is slightly coiled at the apex, as in the abalone (*B*). When the visceral sac is greatly elongate the shell is correspondingly an elongate cone. It is rarely irregularly coiled (Vermetidæ, fig. 362, *C*). It is usually coiled like a watch spring in one plane, or like a spiral staircase; in the latter case the shell is more or less conical (fig. 362, *D*, *E*) and one can speak of its apex and base. In the middle of the base is usually a depression, the umbilicus. Sometimes the coils are loose and do not touch in the axis connecting umbilicus and apex, so that one can look into the space, but usually the coils fuse together into a calcareous pillar, the columella, around which the whorls pass (fig. 362, *E*, *c*).

The shell increases to a certain size by additions from the mantle edge; and since this determines the aperture, the shell is marked with parallel lines of growth. The pigment is elaborated on the edge of the mantle, and in the formation of the shell passes into it, causing its color pattern. When the siphon is present the shell shows a corresponding process. Thus are distinguished holostomate shells with smooth mouths (fig. 362, *D*) and siphonostome shells, in which the anterior margin is drawn out in a groove (fig. 362, *E*).

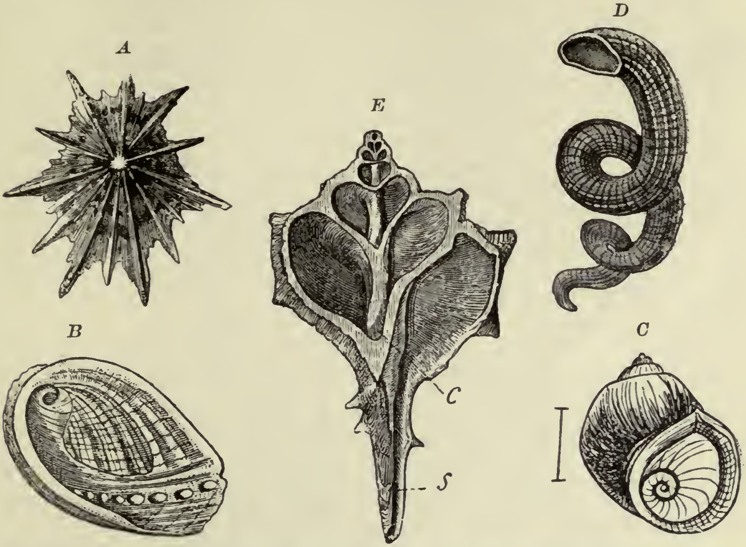


FIG. 362.—Various forms of shells. (After Schmarda, Bronn, and Clessin.) *A*, *Patella costata*; *B*, *Haliotis tuberculata*; *C*. *Vermetus dentiferus*; *D*, *Lithoglyphus naticoides*; *E*, shell of *Murex* opened to show *c*, columella; *s*, siphon.

A simple conical shell without further evidence is not proof of primitive structure. It may arise from the spiral form by degeneration, if the visceral sac be reduced. Thus the shells of *Fissurella* and *Patella* are to be explained, for the viscera here show the results of an earlier spiral twist.

In most places the union between shell and soft parts is not very firm, but the connexion at the aperture is more intimate, while a muscle is attached to the columella (musculus columellaris) at about the middle point of its height, the other end being inserted in the foot. It is for the retraction of the animal within the shell, first the anterior part with the head and then the rest with the metapodium. In this the metapodium is folded so that its dorsal surface lies towards the aperture. Hence in many species this surface secretes a door, or *operculum*, which closes the aperture when the body retracts. Since the aperture increases in size with growth, the operculum must also enlarge, which is accomplished in a spiral manner (fig. 362, *D*), the process sometimes showing in a spiral line on the outside. So-called eye stones are the opercula of small Trochidæ and Turbinidæ. Land snails are usually without opercula, but at certain times, as in hibernation, they can close the shell by a calcareous plate, the *epiphragm.* In the spring this separates from the shell and is lost.

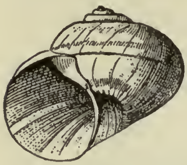


FIG. 363.—Sinistral shell of *Lanistes carinatus.* (From Ludwig-Leunis)

In most gasteropods the shell is coiled to the right, but in some species (fig. 363) the whorls are constantly turned to the left, while reversed specimens occasionally occur in many species which are normally dextral.

In the shell there are at most two layers, an inner lamellar layer (not always present), which sometimes is highly iridescent, and an outer porcellanous layer, which is opaque and contains the pigment. In rare cases the mantle and consequently the shell are lacking, or the mantle is present but the shell is rudimentary and not visible externally because the mantle folds have grown over it. In these cases the visceral sac is not prominent. Since the shell-less forms possess a mantle and shell in the young, the adult conditions are explained by degeneration.

Only a few gasteropods are like the Amphineura and Acephala in being bilaterally symmetrical. Usually the spiral twist of the visceral sac has resulted in a torsion of other parts from left to right, in which alimentary tract, nephridia, gills, heart, and nervous system take part. The intestine is bent in this way, the anus opening into the mantle chamber on the right side, or the twisting may be continued so far as to double the intestine on itself, the anus being in the middle line in front, near the head. Nephridia, gills (with them the osphradia), and heart wander in company, so that the organs primitively belonging on the left side may be trans-

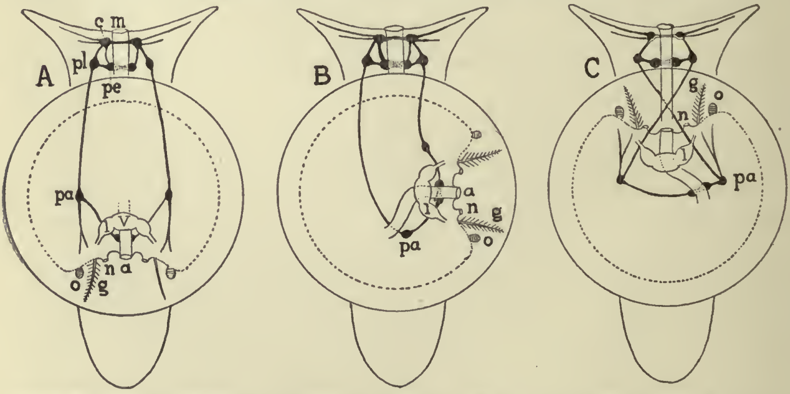


FIG. 364.—Three diagrams illustrating the torsion of the body and the twisting of the nervous system in gasteropods. (After Lang.) *A*, bilateral, *B*, asymmetrical, *C*, streptoneurous condition. The reference letters are placed upon the organs of the primitive left side. *a*, anus; *c*, cerebral ganglion; *g*, ctenidium; *l*, auricle; *m*, mouth; *n*, nephridial opening; *o*, osphradium; *pa*, parietal ganglion; *pe*, pedal ganglion; *pl*, pleural ganglion; *v*, ventricle.

ferred to the right and *vice versa*. With this there is a tendency to asymmetry and the loss of the organs (usually of the primitively left side). When the nervous system takes part in the twisting a notable crossing of the cerebrovisceral commissures takes place, known as streptoneury or chiastoneury (fig. 364, *c*).

The alimentary canal begins with a muscular region which in some groups is developed into a large protrusible proboscis (fig. 365). The pharynx, which follows, contains the tongue, a ventral ridge supported by one or more cartilages and covered by a cuticular layer, the radula or lingual ribbon (odondophore). The upper surface of the radula is armed with sharp, backwardly directed teeth (fig. 366) which are usually arranged in transverse and longitudinal rows, but which vary so in number, form, size, and arrangement that they are of value in classification. Although the radula covers the tongue, it is formed in the radula sac, which lies behind the tongue. From this it grows forward like a nail over its bed as fast as it is worn out in front. It is opposed in eating by a single median or a pair of lateral jaws (lacking in carnivorous forms).

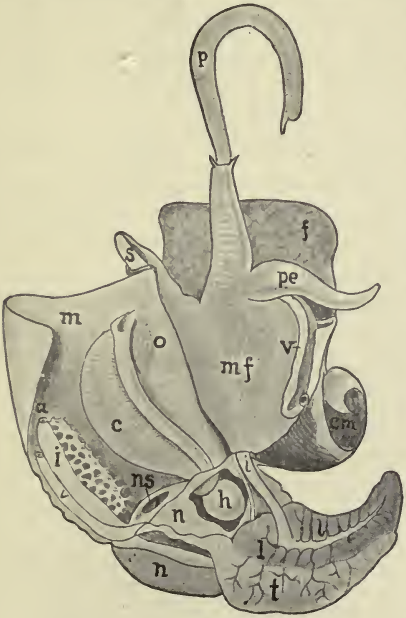


FIG. 365.

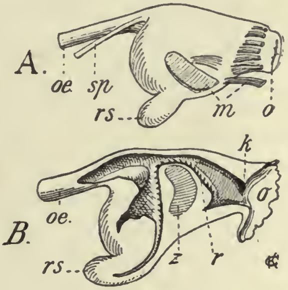


FIG. 366.

FIG. 365.—*Pyrula tuba*, male. (After Souleyet.) The mantle has been cut on the right side and turned to the left, reversing the pallial organs. *a*, anus; *c*, ctenidium; *cm*, columellar muscle; *f*, foot; *h*, heart in pericardium; *i*, intestine; *l*, liver; *m*, mantle; *mf*, floor of mantle cavity; *n*, nephridium; *ns*, opening of nephridium; *o*, osphradium; *p*, proboscis; *pe*, penis; *t*, testes; *v*, vas deferens cut in two.

FIG. 366.—Pharyngeal region of *Helix pomatia*. *A*, side view; *B*, section. *m*, muscle; *oe*, œsophagus; *r*, radula; *rs*, radula sac; *sp*, salivary duct; *z*, lingual cartilage.

The rest of the alimentary canal is convoluted, the anus being usually on the right side in front, in or beside the mantle chamber (figs. 365, 370, 371). Rarely it empties in the middle line behind.

Œsophagus, stomach, and intestine are slightly marked off from each other. The convolutions of the intestine are enveloped by the liver, which by its large size forms the chief part of the visceral sac. A pair of salivary glands empty into the pharynx, these in the Doliidæ secreting free sulphuric acid.

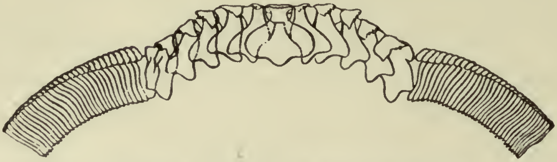


FIG. 367.—Row of teeth from the radula of *Trochus cinerarius*. (After Schmarda.)

The nervous system usually differs from that of other molluscs in that the pleural and parietal ganglia are free (p. 353). If the commissures be short, the ganglia are collected near the pharynx and, thus freed from the body torsion, are symmetrical (orthoneurous, fig. 368, *II*). If the cerebrovisceral commissure be longer, the result is almost always streptoneury (chiastoneury). Pleural and visceral ganglia hold their place, but the right parietal ganglion crosses above the intestine to the left side (hence called supra-intestinal), while the left passes under the intestine to the right side (subintestinal), the cerebrovisceral commissure being twisted like the figure 8. The strong development of the pharynx is accompanied by buccal ganglia. The existence of streptoneurous forms among the orthoneurous Opisthobranchs (*Actæon*) and Pulmonata (*Chilina*) shows that orthoneury in these groups has arisen from streptoneury.

Gills, heart, and nephridia are best treated together. Certain genera (*Haliotis, Fissurella*) recall the Acephala in having these organs in pairs, while the intestine passes through the heart. As a rule the asymmetry induced by the torsion of the body has resulted in the loss of the ctenidium, osphradium, nephridium, and auricle of one (the primitively left) side. Prosobranchs and Opisthobranchs are recognized accordingly as the gills are on the anterior or posterior part of the body. In the Opisthobranchs (fig. 369) the ctenidia have been lost and are replaced by secondary gills on the back. Here the heart is in front of the gills; it receives blood from behind and forces it forward to the head by an aorta. In the Prosobranchs the heart has been twisted about ninety degrees, so that the auricle is in front and the ctenidium in front of this (fig. 370), while the aorta leads backwards. The nephridium, which communicates with the pericardium by a nephrostome, is rarely a racemose gland; usually it is saccular, the lumen bearing gland cells and concretions; its duct either empties into the mantle cavity or beside the anus.

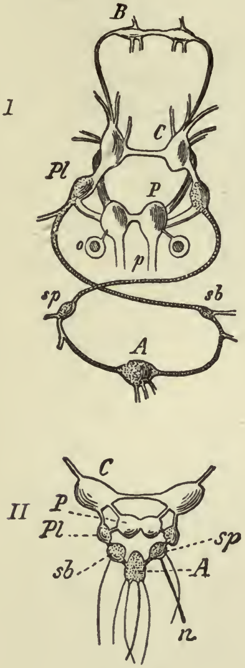


Fig. 368.

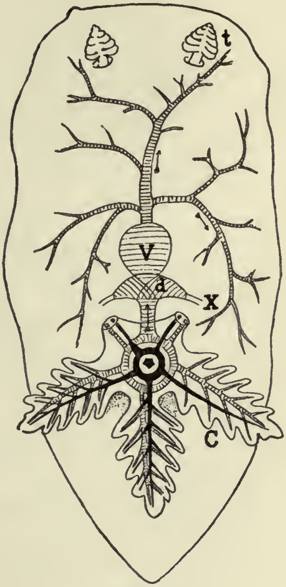


Fig. 369.

Fig. 368.—*I*, streptoneurous nervous system of *Paludina*. (After Hering, from Gegenbaur.) *II*, orthoneurous system of *Limnœa*. (After Lacaze-Duthiers.) *A*, visceral; *B*, buccal; *C*, cerebral; *p*, pedal; *Pl*, pleural; *sb*, *sp*, sub- and supra-intestinal ganglia; *n*, olfactory nerve; *o*, otocyst.

Fig. 369.—Diagram of circulation in *Doris*. (After Leuckart.) *a*, auricle; *c*, gills around anus; *t*, tentacle; *v*, ventricle; *x*, vessels returning venous blood from the body.

The sexual organs in some forms (Cyclobranchs and many Zygobranchs) empty into the nephridia. They show two extremes. On the one hand are completely diœcious species, on the other there may be complete hermaphroditism (many Tectibranchs, Pteropoda), in which the male and female organs are united throughout their extent. Intermediate stages occur; those of the pulmonates are described below.

In the Helicidæ there is a hermaphrodite gonad which lies together with the liver in one of the first whorls of the shell (fig. 371, *z*). A coiled genital duct follows which widens to a thick-walled 'uterus' (*u*) along which a second seminal canal appears to lie. Actually in the interior there is but a single lumen, the different appearances being due to glands in the walls. A separation into vas deferens and vagina occurs at the end of the uterus. The vas deferens (*vd*) proceeds as a small coiled canal to the genital pore. Here it enlarges to a protrusible penis (*p*) with which is connected a retractor muscle and an appendage, the flagellum (*fl*). The vagina is broader and goes straight to the genital pore, where it meets the penis. Connected with the female genitalia are the large albumen gland (*ei*) at the beginning of the uterus and a receptaculum seminis (*r*); a round vesicle connects with the vagina by a long duct, and (not always present) two 'finger-form glands.' Lastly, the dart sac (*ps*) of the vaginal wall, which secretes a calcareous stylet, the 'love dart,' which in copulation acts as a stimulus to the male genitalia. In spite of hermaphroditism a copulation lasting for days may occur, connected with which is the fact that in many species the male cells are first matured, then the female (proterogyny); or the reverse may occur (proterandry).

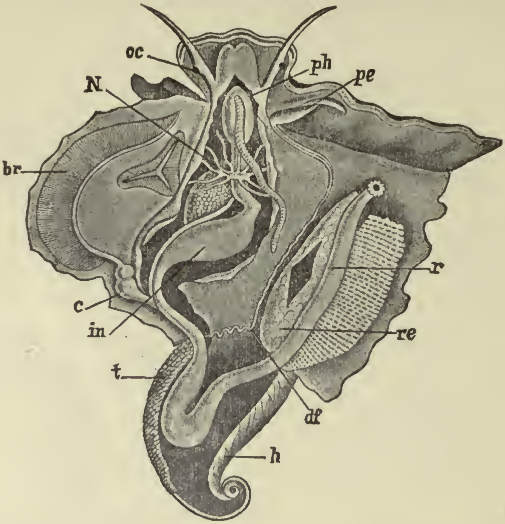


Fig. 370.—Anatomy of *Cypræa tigris.* (After Quoy et Gaimard.) *br*, ctenidium; *c*, heart; *df*, vas deferens; *h*, liver; *in*, stomach; *N*, cerebral ganglion; *oc*, eye; *pe*, penis; *ph*, pharynx, the radula drawn out; *r*, rectum; *re*, nephridium; *t*, testes.

The sexual opening is almost always on the right side, beside the anus or in front of it on the head. Its position may be recognized in hermaphroditic species and in diœcious males by the grooved dermal fold, the penis (fig. 370, *pe*). Occasionally this is separated from the genital pore, but is connected with it by a ciliated groove.

The terrestrial snails lay their large tough-shelled eggs in damp earth; in the aquatic forms the eggs are laid in masses, usually gelatinous, each egg with a layer of albumen and a firm shell. Occasionally there is a kind of nest, as is the case with *Ianthina* which carry the mass of eggs, attached to the foot, about with them. A few gasteropods are viviparous.

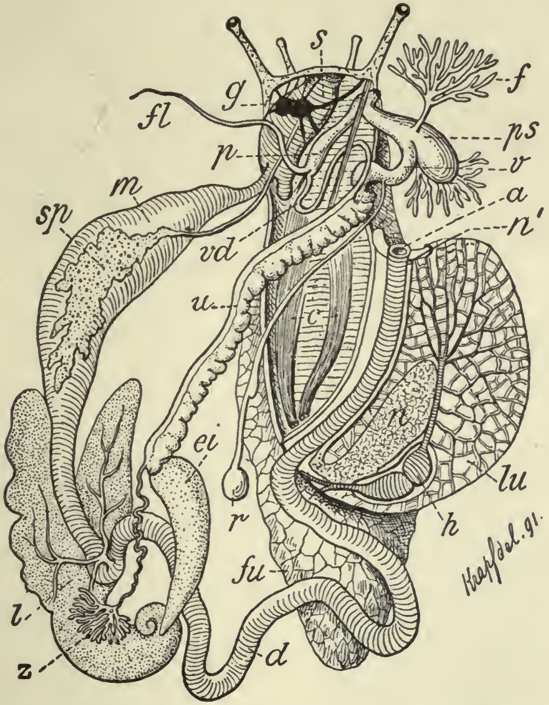


FIG. 371.—Anatomy of *Helix pomatia*, the roof of the pulmonary sac cut at the left side and turned to the right; the pericardium and visceral sac opened and the viscera separated. *a*, anus; *c*, columellar muscle; *d*, intestine; *ei*, albumen gland; *f*, finger-form gland; *fl*, flagellum; *fu*, foot; *g*, cerebral ganglion; *h*, heart; *l*, liver; *lu*, lung; *m*, stomach; *n*, nephridium; *n'*, its opening; *p*, penis; *ps*, dart sac; *r*, receptaculum seminis; *s*, pharynx; *sp*, salivary gland; *u*, uterus; *v*, vagina; *vd*, vas deferens; *z*, hermaphrodite gonad.

In the development the great constancy with which the veliger stage (figs. 342, 343) appears is noticeable. Most marine larvæ swim by their velum (often divided) at the surface before creeping at the bottom. But in those cases where the snail leaves the egg in the definitive condition the velum is usually developed in embryonic life, sometimes so strongly that the embryo rotates in the surrounding fluid.

Order I. Prosobranchia.

The Prosobranchs, like most gasteropods, have the twisting of the visceral complex from left posterior to right anterior, so that the anus lies on the right side near the head, the nervous commissures are twisted into an 8, and the nephridia of the right side have been carried to the left, where they lie far forward. This has twisted the heart so that it receives branchial blood from in front and sends it backwards through the aorta. The sexes are separate and the shell and mantle are usually well developed. Accordingly as the mantle is drawn out in a siphon or not, the shells are siphonostomate or holostomate (p. 371). Certain Prosobranchs are near the primitive Amphineura in the retention of both ctenidia, both auricles, and both nephridia, but in the great majority only one gill (the primitive right) is present and the corresponding auricle alone is well developed, although the other may exist in a rudimentary condition.

Sub Order I. ASPIDOBRANCHIA (Diotocardia, Scutibranchia). Ctenidium bipectinate (fig. 372) or absent. There are usually two auricles and two nephridia. DOCOGLOSSA (limpets), auricle single; one or no ctenidium; intestine not passing through heart, shell conical. Acmæidæ with ctenidium. *Acmœa** (fig. 373). Patellidæ, ctenidia lacking, replaced by a ring-like mantle gill. *Patella* (fig. 362, *A*). ZYGO-

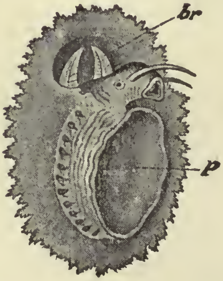


Fig. 372.

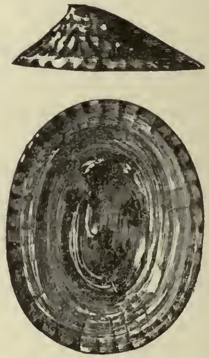


Fig. 373.

Fig. 372.—*Fissurella patagonica*, ventral view. (From Bronn.) *br*, the paired gills; *p*, foot.

Fig. 373.—*Acmœa testudinalis*,* limpet. (From Binney-Gould.)

BRANCHIA. Two ctenidia (fig. 372), shell with marginal slit or with holes corresponding to an anal notch in the mantle; auricles and nephridia paired; heart traversed by intestine. Fissurellidæ, keyhole limpets; shell conical, with apical opening. Haliotidæ, abalones; shell weakly spiral, flat, with a series of holes. *Haliotis** (fig. 362, *B*). AZYGOBRANCHIA. One ctenidium, but two auricles. Trochidæ, operculum horny; *Trochus*, *Margarita.** Turbinidæ, top shells; operculum calcareous. *Turbo*, *Phasianella.*

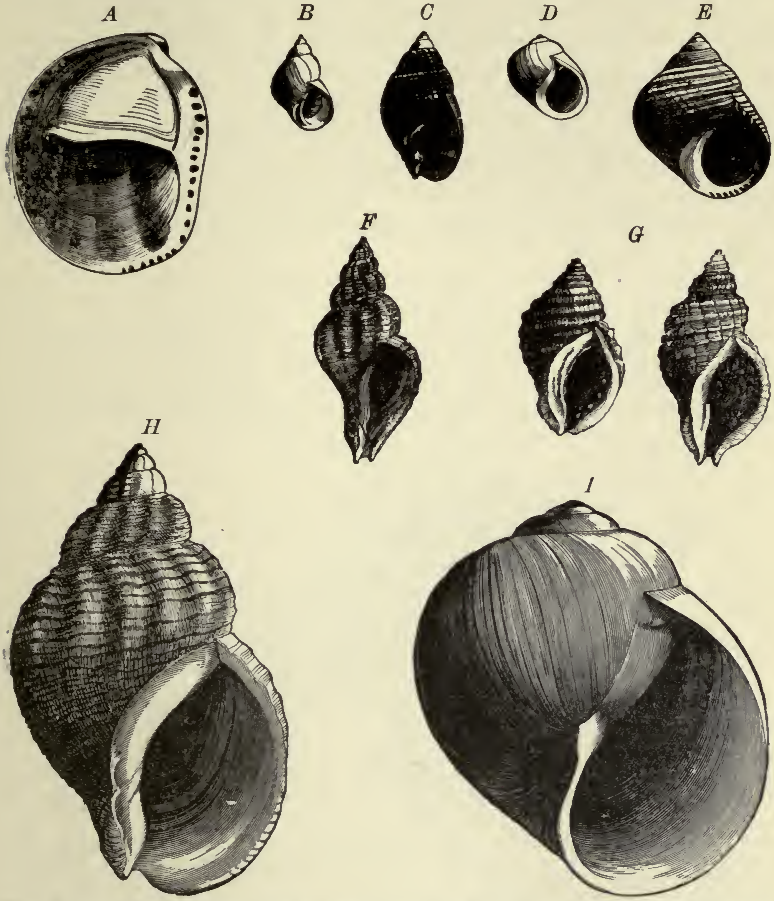


Fig. 374.—American Pectinibranch gasteropods. (From Binney-Gould.) *A*, *Crepidula fornicata*; *B*, *Lacuna vincta*; *C*, *Ilyanassa obsoleta*; *D*, *Littorina palliata*; *E*, *L. litorea*; *F*, *Urosalpinx cinerea*; *G*, *Purpura lapillus*; *H*. *Buccinum undatum*; *I*, *Lunatia heros.*

Sub Order II. PECTINIBRANCHIA (Monotocardia, Ctenobranchia). Ctenidium unipectinate, osphradium well differentiated (fig 365), intestine not passing through the heart. Many groups are recognized, based upon the structure of the lingual ribbon. Of the thousands of species only a few groups can be included here. RHACHIGLOSSA; siphonostomate, predatory. MURICIDÆ (*Murex*, *Purpura*,* *Urosalpinx**) have an anal gland secreting a substance first colorless, turning to purple by exposure to air. The Tyrian purple was produced by *Murex trunculus*. *Urosalpinx cinereus** drills into oysters. BUCCINIDÆ, whelks, VOLUTIDÆ, and OLIVIDÆ belong here. TOXIGLOSSA; CONIDÆ, with large œsophageal poison gland, some species producing severe wounds. *Conus*, tropical; *Bele.** TÆNIOGLOSSA; NATICIDÆ, *Neverita*,* and *Lunatia*,* common snail of Atlantic coast, their egg-masses being the familiar sand saucers. LITTORINIDÆ; periwinkles. CYPRÆIDÆ, cowries; *Cypræa moneta* of India is used as money in Africa. AMPULLARIDÆ; amphibious, part of branchial cavity acting as lung, part containing ctenidium. PALUDINIDÆ, fresh water. CYCLOSTOMIDÆ, tropical terrestrial forms, the mantle cavity a lung.

HETEROPODA. In all details of gills, genitalia, heart, and nervous system these are true Pectinibranchs, but from an exclusively pelagic life have acquired peculiar modifications. As in most pelagic animals the body is gelatinous and transparent. The head is elongate, and the body is enlarged so that usually it cannot be retracted into the shell. Most characteristic is the division of the foot into pro- and metapodium (fig. 375), the latter forming a tail-like elongation of the body. The propodium is vertically flattened and by its undulations serves as a swimming organ. The Heteropoda are predaceous and extremely voracious; they swim back downwards. The ATLANTIDÆ can completely withdraw into the shell and close it with an operculum; the CARINARIIDÆ (fig. 375) have a shell which scarcely covers the visceral complex; the PTEROTRACHEIDÆ have no shells.

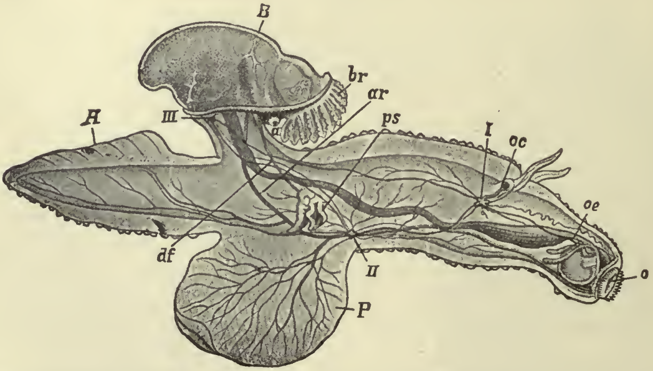


FIG. 375.—*Carinaria mediterranea* (after Gegenbaur), shell removed. *A*, metapodium; *a*, anus; *ar*, aorta; *B*, visceral sac; *br*, branchiæ, the heart above; *df*, vas deferens; *o*, mouth; *oc*, eye with tentacle; *œ*, œsophagus; *p*, propodium; *ps*, penis; *I*, *II*, *III*, cerebral, pedal, and visceral ganglia.

Order II. Opisthobranchia.

The Opisthobranchia have not varied from the primitive symmetry to such an extent as have Prosobranchs and Pulmonates. The anus is in the plane of symmetry or only slightly removed from it, although it may be placed far forwards. The nervous system is orthoneurous, the twist being straightened (except in Actæonidæ). The heart also retains its primitive position, receiving blood from behind and forcing it forward to the body through the aorta (fig. 369). In rare cases a (right) ctenidium, a poorly developed mantle, and a thin shell enveloped in the latter occur. Usually these have been lost and the place of the ctenidium is taken by accessory gills of various forms or a dermal respiration occurs. It is interesting to note that the larvæ have well-developed mantle and shell. Also important from the systematic standpoint is the existence of hermaphroditism, the genital duct opening on the right side. Many of the Opisthobranchs afford fine examples, in form and coloration, of protective resemblance. All are marine.

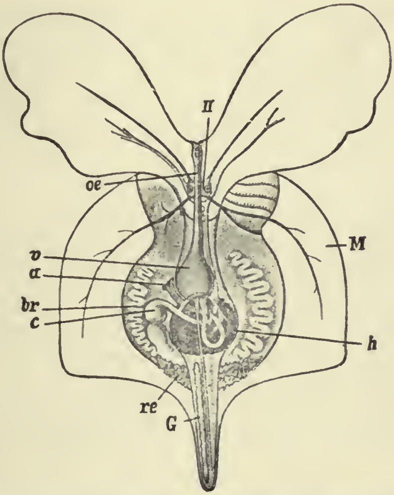


FIG. 376.—*Hyalœa complanata* from above. (After Gegenbaur.) *a*, arms; *br*, gill; *c*, heart; *g*, gonad; *h*, liver; *m*, mantle; *oe*, œsophagus; *re*, nephridium; *v*, stomach; *II*, pedal ganglion and otocyst.

Sub Order I. TECTIBRANCHIA. Mantle and usually a shell and ctenidium present, parapodial processes often present. *Scaphander*,* *Bulla*,* *Philine*,* *Aplysia*.

Sub Order II. PTEROPODA. Pelagic forms which in most points of structure agree with the Tectibranchs. The head and usually eyes and tentacles are lacking, while the fins (in reality greatly developed parapodia) are highly characteristic, giving the name 'wing-footed' to these forms. Like the Tectibranchs they are hermaphroditic, orthoneurous, have a single ctenidium and a posterior auricle. The THECASOMATA have shells, those of Limacinidæ (spiral) and Hyaleidæ (pyramidal) being calcareous. The Cymbulidæ have transparent gelatinous pseudo-shells formed by the subepithelial connective tissue. The long nearly cylindrical shells of the Cavolinidæ make up much of the 'pterpod ooze' of the deep seas. GYMNOSOMATA; shell lacking. *Pneumodermon*, with suckers like those of cephalopods on the proboscis. *Clione*,* arctic.

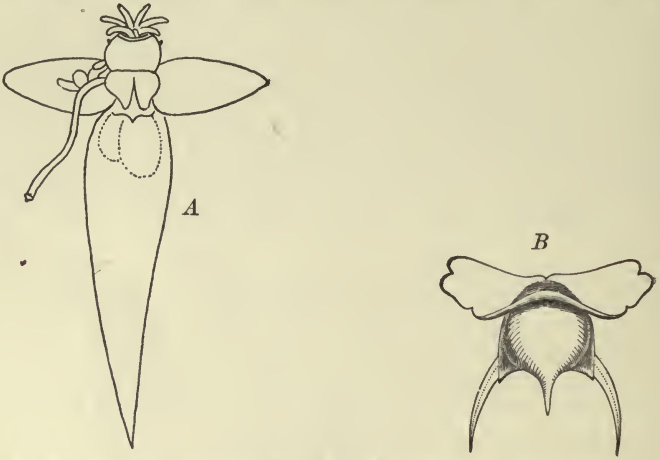


Fig. 377.—*A*, *Clione papilionacea*; *B*, *Hyalea tridentata*. (After Verrill.)

Sub Order III. NUDIBRANCHIA. Shell, ctenidia, and osphradia lacking; most possessing accessory gills (or cerata) of varying form and distribution. In the Doridiidæ they form a cluster of retractile bushes around the anus (fig. 378). In the Tritoniidæ they are in two rows, right and left (often branched) upon the back. The Æolidæ have several rows (*Dendronotus**), while in the Elysiidæ cerata are lacking. The Æolidæ are noteworthy in having nematocysts like those of the cœlenterates (p. 229).

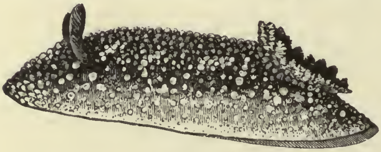


Fig. 378.

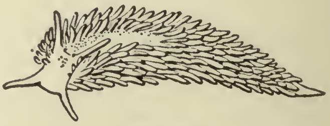


Fig. 379.

Fig. 378.—*Doris bilamellata*.*
Fig. 379.—*Æolidia papillosa*. (From Ludwig-Leunis.)

Order III. Pulmonata

In several respects the Pulmonata are intermediate between the Prosobranchs and Opisthobranchs. Like the latter they are orthoneurous and hermaphroditic (p. 376). On the other hand the respiratory organ is far forward near the head, with the result here, as in the Prosobranchs, that the auricle is forward, the aorta behind. The opisthopneumous Testacellidæ have the lungs at the posterior end of the body. Here and there streptoneurous conditions occur (*Chilina*).

The lung, the most characteristic feature of the order, is a spacious sac arising from the mantle cavity along with the degeneration of the ctenidium. It begins on the right side and like a half-moon stretches some distance on the left. On the right side is a small opening, the spiracle, with a sphincter muscle, and in its margin the anus and sometimes the ureter. The roof of the lung is occupied by a rich network of blood vessels (fig. 371, *lu*) which draw the blood from a marginal vein, collect it in a main trunk and carry it to the heart.

Many pulmonates are aquatic, but since they have no gills they must occasionally come to the surface to fill the lung sac with air. This is the case with many pond snails of the Limnæidæ, but some, which live at great depths, as in the lakes of Geneva and Constance, and consequently cannot reach the surface, use the skin and to some extent the lung for water-breathing. Several genera (*Planorbis*, *Pulmobranchia*, *Siphonaria*) have given rise to secondary gills.

Sub Order I. STYLOMMATOPHORA. Four retractile tentacles, the eyes being borne at the tips of the second and longer pair. The HELICIDÆ have a well-developed shell, closed by an epiphragm (p. 372) during hibernation. *Helix*,* many hundred species distributed among many sub genera. *Pupa*,* *Achatina*, *Bulimus*, many tropical species. LIMACIDÆ. Shell reduced, completely concealed in the mantle. *Limax*,* *Arion*,* *Ariolimax*.*

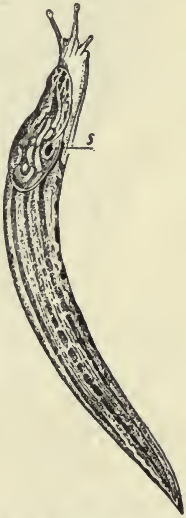


FIG. 380.—*Limax cinereus*. (After Ludwig-Leunis.) *s*, spiracle.

Sub Order II. BASSOMATOPHORA. Only one pair of non-retractile tentacles, the eyes at their base. LIMNÆIDÆ, pond snails, living in shallow ponds and brooks. *Limnæa*,* *Planorbis*.*

Class V. Cephalopoda.

The Cephalopoda are distinguished among the molluscs by their size and their high organization. The majority measure, including the arms, from eight inches to three feet in length, a few are smaller (two to seven inches), while especially rare are the huge giants, some of which may be over forty feet in length. These large species for a long time were only known from the tales of sailors, who said that the animals had grasped vessels with their large muscular arms and had drawn them into the sea. In the last half-century some of these forms, belonging to the genus *Architeuthis*, have been stranded by storms on the coasts of Newfoundland and Japan. One of these Newfoundland specimens had a body twenty feet long from head to tail, and one of the arms was thirty-five feet in length. Since these arms are composed entirely of muscle, it is easily conceivable that they might swamp a small vessel.

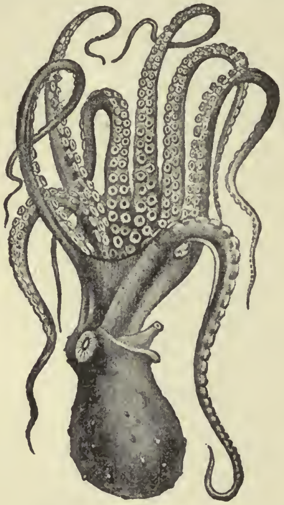


Fig. 381.

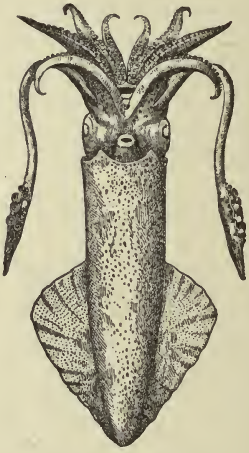


Fig. 382.

Fig. 381.—*Octopus tonganus* from the side. (After Hoyle.) Funnel and mantle fold to the right; back and eyes on the left.
Fig. 382.—*Loligo kobiensis*, ventral view. (After Hoyle.)

The body of a cephalopod is divided by a constriction into head and trunk. At the extremity of the head is the mouth, and around this a circle of arms or tentacles. Each tentacle is tapering and bears on its oral surface rows of suckers (in some species altered to hooks). The Octopoda have eight of these arms, all equal in size (fig. 381), four on the right side, four on the left. The Decapoda (fig. 382) have in addition two longer arms which bear suckers only on the enlarged tips and can be retracted into special pouches. This additional pair come between the third and fourth of the Octopoda, counting from the dorsal side.

Behind the crown of tentacles are, right and left, the pair of large eyes which superficially closely resemble those of the vertebrates, since they have a transparent cornea and a large pupil surrounded by an iris. Internally the resemblance is not less pronounced (fig. 383). Behind the iris is a lens and a vitreous body, the latter being bounded by the retina and this in turn by a pigmented silvery layer, the argentea or choroid, which contains cartilages recalling the sclerotic coat. Two striking peculiarities separate these eyes from those of the vertebrates and show that they have arisen independently and have an entirely different developmental history. (1) The cornea in many species has an opening by which water enters the anterior chamber; (2) the layer of rods in the retina abuts against the vitreous body and the ganglionic layer lies behind, while in the vertebrates the reverse is the case.

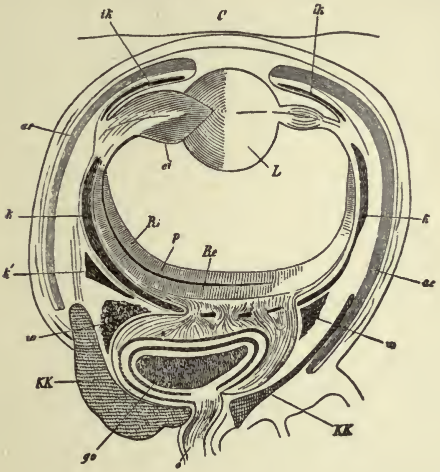


FIG. 383.

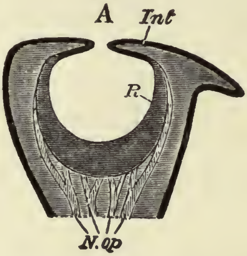


FIG. 384.

FIG. 383.—Diagrammatic section of Cephalopod eye. (After Gegenbaur.) *ae*, argentea (choroid); *C*, cornea; *ci*, ciliary process; *go*, optic ganglion; *ik*, iris; *k*, cartilages; *L*, lens; *p*, pigment layer; *Re*, cellular layer of retina; *Ri*, rod layer of retina; *w*, white body.

FIG. 384.—Schematic section of eye of *Nautilus*. (From Balfour.) *A*, aperture of optic cup; *Int*, iris-like fold of integument; *N.op*, optic nerve; *R*, retina.

The foregoing description applies to but part of the Cephalopoda. The highly different Nautilidæ have a large number of lobe-like processes on the head, these without suckers. The eyes are deep pits, opening to the exterior by a small aperture, the base of the pit being occupied by the retina, while lens, vitreous body, iris, and cornea are lacking (fig. 384). It is to be noticed that the other cephalopod eyes pass through a *Nautilus* stage.

In the trunk anterior and posterior sides are distinguishable, the two passing into each other on the sides. The anterior side (which corresponds only in part to the ventral side of other molluscs) is wholly covered by the mantle, a strong muscular fold, which takes its origin from the periphery of the body, often encroaching upon the back and always terminating with free margins at the head. On opening the mantle by a ventral incision (fig. 385) the two ctenidia (four in *Nautilus*) are seen on either side.

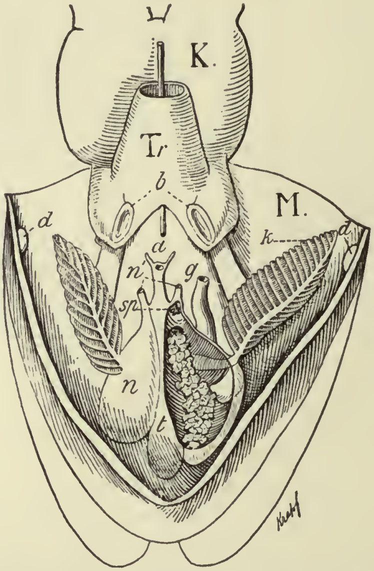


Fig. 385.—*Sepia officinalis*, the mantle and left nephridial sac opened to show the vena cava leading to the branchial heart. *a*, anus; *b*, *d*, lock of siphon and mantle; *g*, genital opening; *K*, head: *k*, ctenidium ; *n*, nephridial sac ; *n′*, nephridial opening ; *sp*, nephrostome ; *t*, ink sac ; *Tr*, siphon.

Between them in the middle line is the anus, and right and left of this and a little behind are the nephridial openings (four in *Nautilus,* which also has osphradia). More laterally are the sexual openings, of which one (usually the right) is commonly absent.

At the head the mantle opens by a slit to the exterior, but it can be closed and fastened by various locking contrivances (in Sepia, Loligo, etc., by button-like projections (fig. 385, *d*) which fit into corresponding sockets (*b*) on the trunk). When thus closed the communication with the exterior is by a special conical muscular tube, the funnel or siphon, which is fastened to the body and has a wide mantle aperture. Since the cephalopods, by contraction of the mantle wall, can drive the water from the mantle cavity through the siphon with great force, they can swim very rapidly by the reaction. Here, too, *Nautilus* is peculiar in that the siphon is throughout life composed of two overlapped folds, which is significant since in the embryos of other forms the siphon (fig. 396) arises as two separate folds which later unite to produce the definitive condition. A typical foot is lacking, but comparative morphology shows that the siphon is composed of a pair of epipodia, while the arms are differentiations of fused foot and head.

Head and trunk are covered with a thin mucous skin, which shows in a marked degree the power of changing color. *Loligo* will pass from a dark red to a translucent white; *Octopus* has an even greater gamut of color. These color changes are possible since in the cutis there is a silvery layer over which are numerous different-colored pigment cells or *chromatophores*, in which radial muscle fibres are inserted. On contraction of these the chromatophores are flattened and thus influence the color; when the fibres relax the pigment cells contract to small spots. In deep-sea cephalopods phosphorescent organs have been observed.

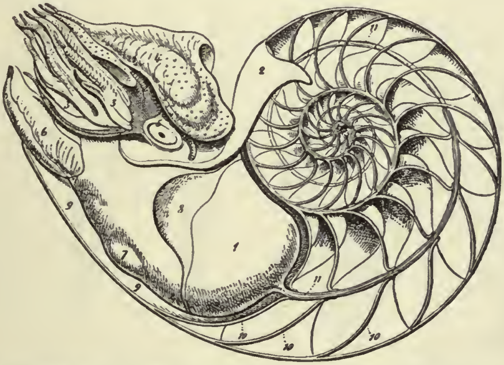


FIG. 386.—Female *Nautilus*, the shell bisected. (From Ludwig-Leunis.) *1*, mantle; *2*, dorsal lobes; *3*, tentacles: *4*, head fold; *5*, eye; *6*, siphon; *7*, position of nidamental gland; *8*, shell muscle; *9*, living chamber; *10*, partitions between chambers; *11*, siphuncle.

Notwithstanding the soft bodies a well-developed shell occurs in living cephalopods only in *Nautilus* and *Argonauta* (figs. 386, 398). Externally the shell of the former, coiled in a plane, resembles that of certain snails like *Planorbis;* but on section it is seen to be divided by partitions into numerous chambers which increase in size towards the aperture. Only in the last is the animal situated; the others are filled with air. Each partition has a small opening, and through these runs a strand of tissue, the siphuncle. Among the fossil cephalopods many forms—the Nautiloids and Ammonites—have a similar chambered shell; but in other recent forms and in many extinct species the shell has undergone a more or less complete degeneration. In *Spirula peronii* (the animals of which are extremely rare, the dead shells common) there is a similar chambered shell, buried in the mantle (fig. 387). In the Decapoda the equivalent of the shell is completely concealed in the back of the animal. In the *Sepias* it is a lamellar calcareous structure, the well-known cuttle bone; in the

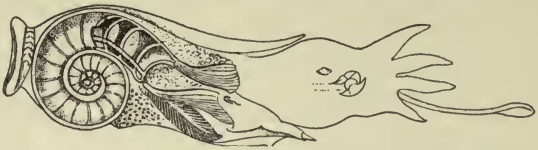


FIG. 387.—*Spirula*, with internal shell. (After Owen.)

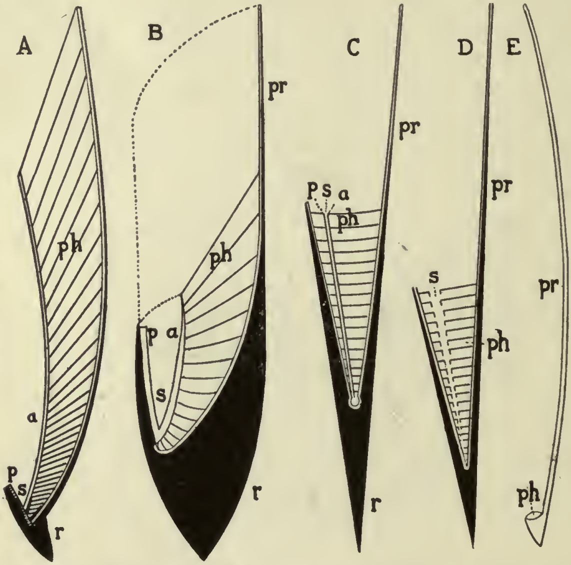


FIG. 388.—Diagram of shells, etc. of various cephalopods. (After Lang.) *A*, *Sepia;* *B*, *Belosepia;* *C*, *Belemnites;* *D*, *Ostracoteuthis;* *E*, *Ommastrephes*. *a*, anterior; *p*, posterior; *ph*, phragmocone; *pr*, proostracum; *r*, rostrum; *s*, siphon.

Loliginidæ it forms a 'pen' of purely organic nature (fig. 340, *A*). Like true shell these dorsal structures are products of the external epithelium, only the epithelium which forms them, the shell gland, has become folded in and the walls have united over it.

The shell of *Argonauta* (fig. 398) is different. It occurs only in the female, is thin as paper, spirally coiled at the tip, and is only in part a secretion of the body, for a part of it is formed by two tentacles which are expanded for this purpose. Internal partitions are lacking, and this shell serves as a nest for the eggs. A word or two may be added to correlate the recent and fossil shells of the Dibranchiata, which are always internal and more or less rudimentary. The fossil Belemnites (fig. 388, *c*) had a chambered shell ('phragmocone') perforated for the siphuncle. In front this is prolonged ventrally into a thin broad plate, the proostracum, while behind it is inserted in a calcareous sheath, the guard or rostrum. From this, by comparison with the fossil *Belosepia* (*B*), it is seen that the cuttle bone as it appears in commerce (*A*) is the anterior part of the chambered shell, its laminæ being the partitions, while in the animal the rostrum and siphuncle are in part retained. On the other hand, comparison with the fossil *Ostracoteuthis* (*D*) shows that in *Ommastrephes* (*E*) we have but a remnant of the phragmocone, while the bulk of the pen is proostracum. In *Loligo* the phragmocone is entirely lacking.

The mouth, situated in an oval buccal mass, lies between two horny jaws, like the beak of a parrot (fig. 389); then follows a pharynx with a radula, and in turn a long œsophagus, often with a crop-like dilatation. The œsophagus opens into a wider pouch, the stomach, with which is connected a blind sac, frequently coiled. Here the tract doubles on itself and goes straight to the anus, or makes one or two convolutions in its course (fig. 390). One or two salivary glands (upper and lower, the latter poisonous in *Octopus*) open into the œsophagus, and a pair of liver sacs (frequently fused) open by two bile ducts into the gastric blind sac. These ducts may bear racemose glands called the pancreas. Lastly, the ink sac opens into the intestine near the anus. This gland, which has a duct of varying length, secretes in its interior a brownish or blackish pigment. When alarmed the animal ejects this secretion and clouds the water so that it can escape unseen. This organ is best developed in *Sepia officinalis*, and its secretion forms the basis of the well-known color, sepia. *Nautilus* has no ink sac.

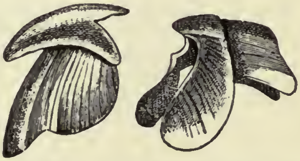


FIG. 389.—Jaws of *Sepia officinalis*.

Just behind the buccal mass are the closely united chief gan-

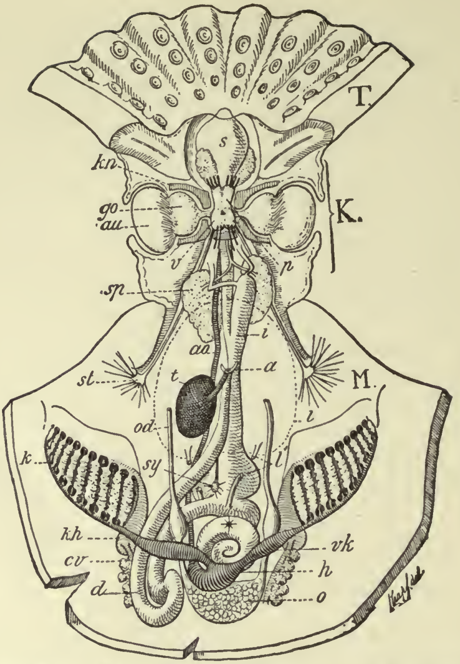


FIG. 390.—Anatomy of *Octopus vulgaris.* *a*, anus; *ao*, aorta; *cv*, vena cava with nephridial appendage; *d*, intestine; *go*, optic ganglion; *h*, systemic heart; *i*, crop; *K*, head; *k*, ctenidia; *kh*, branchial heart; *kn*, cartilage; *l*, *l'*, liver and gall duct, the liver indicated by dotted line; *M*, mantle; *o*, ovary; *od*, oviduct; *p*, pedal ganglion; *s*, buccal mass with salivary glands; *st*, stellate ganglion; *sy*, stomach and sympathetic ganglion; *T*, basis of tentacles; *t*, ink sac; *v*, visceral ganglion; *vk*, auricle of systemic heart; *, spiral blind sac.

glia of the nervous system (fig. 391). A single dorsal mass represents the cerebral ganglia; connected with this by broad commissures, the pedal and visceral (visceropleuro-parietal) ganglia lie close together ventrally. With these parts are associated upper and lower buccal ganglia. The large optic ganglia, developed in the optic nerve arising from the cerebrum, are especially characteristic of the Cephalopoda, as are the ganglia stellata, right and left at the anterior edge of the mantle (fig. 390), which owe their name to the radiation of fibres to innervate the mantle. An unpaired sympathetic ganglion lies at the junction of stomach and blind sac. Cerebral, pedal, visceral and optic ganglia are enclosed in the cephalic cartilage,

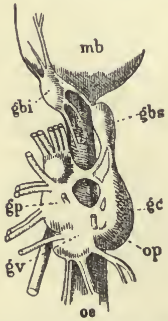


FIG. 391.—Nervous system of *Sepia officinalis* from the side. *gbi*, inferior buccal ganglion; *gbs*, superior buccal ganglion; *gc*, cerebral ganglion; *gp*, pedal ganglion; *gv*, visceral ganglion; *mb*, buccal mass; *œ*, œsophagus; *op*, optic ganglion.

which has the shape of a ring with wing-like processes. The otocysts lie in the ventral arch of the ring. Two pits opening behind the eye are regarded as olfactory, while *Nautilus* has, besides osphradia, two pairs of ciliated optic tentacles.

Most noticeable of the circulatory structures is the presence of two kinds of hearts (fig. 390). The systemic heart consists of two (four in *Nautilus*) auricles receiving the blood from the gills, and a median ventricle from which arise anterior and posterior aortæ. Then there is a branchial heart at the base of each ctenidium which receives the blood from the vena cava and pumps it into the gill. Of venæ cavæ there are an anterior unpaired and two posterior paired trunks, the former dividing and sending a branch to each branchial heart. These trunks are of importance in connexion with the nephridia. The nephridial openings (p. 386) lead to two spacious sacs through which the veins pass obliquely, this part of the blood vessels being enclosed by diverticula of the lumen, covered with epithelial excretory cells. Near its mouth each nephridial sac communicates by a nephrostome with the usually large cœlom (pericardium, gonads, etc.).

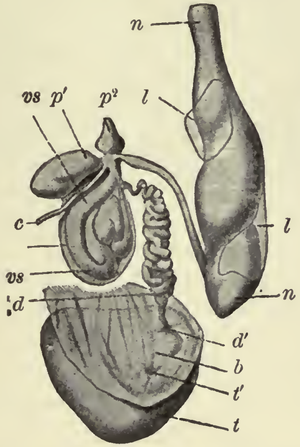


FIG. 392.—Male sexual organs of *Sepia officinalis*. (After Grobben.) *b*, cœlomic sac passing to the left and above into the pericardium; *c*, cœlomic canal to the vas deferens; *d*, vas deferens; *d′*, its opening to cœlom; *l*, portions of cœlom; *n*, Needham's pocket; *n′*, its mouth; *p′*, *p²*, prostates; *t*, testis; *t′*, its opening to cœlom.

In the Octopoda the cœlom is reduced to the gonads and narrow canals leading from the nephrostome to the gonads and branchial hearts, but elsewhere there is a well-developed system of connected cavities (in *Nautilus* opening by two pores into the mantle cavity), consisting of the pericardium around the systemic and branchial hearts and the thin-walled genital sac, one wall of which bears the genital ducts, while on the other the sexual cells arise or the ducts of a separate sexual gland open (fig. 392).

The gonads of the always diœcious Cephalopoda are unpaired and lie far back in the visceral sac. The ducts in the female Octopoda (rarely in the males) and in some Decapoda (Oigopsida) are paired. In *Nautilus* only the right duct is functional in either sex, although the left is well developed. Elsewhere there is only the left duct. The oviducts are saccular with glandular walls; independently of them two pairs of glands open to the exterior, the accessory glands and the large nidamental glands. The vas deferens (fig. 392) is more complicated. It has swellings known as seminal vesicle, prostate, and Needham's sac, in which the spermatophores are stored. These have such a complicated structure and show such motions when swollen with water that they were long regarded as parasitic worms (fig. 393).

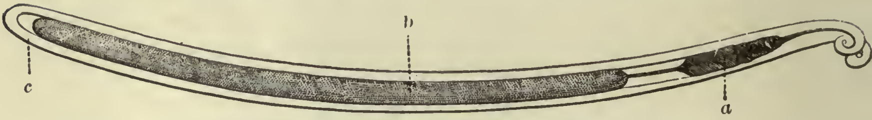


FIG. 393.—Spermatophore of *Sepia*. (From Hatschek, after Milne Edwards.) *a*, discharging apparatus; *b*, packet of spermatozoa; *c*, envelope.

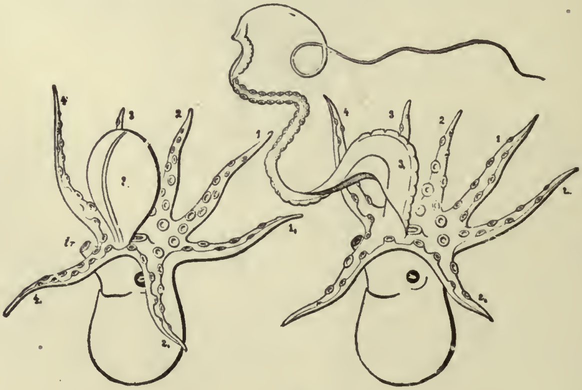


FIG. 394.—Male of *Argonauta argo*. (After Müller, from Hatschek.) *1–4*, arms of right side; *1.–4.*, arms of left side; *3*, hectocotylised arm, at the left in its sac, at the right protruded.

The spermatophores are conveyed to the female by means of more or less modified (hectocotylised) arms of the male. In a few genera the proper tentacle becomes a 'Hectocotylus' (fig. 394).

It swells at its base to a sac in which the peripheral end is enclosed. This part contains a canal for the spermatophores, cuts loose from the male, and can creep about for days in the mantle chamber of the female. Since it appears as if an independent animal, it was first described as a parasitic worm under the name *Hectocotylus*. Later it was regarded as a rudimentary male cephalopod.

The eggs are either fastened singly to aquatic plants or are laid in large gelatinous masses. They are rich in yolk, and in consequence undergo partial discoidal segmentation (fig. 103). The blastoderm, on the end of the oval egg, forms the anlagen of the separate organs (eyes, arms, siphon, and

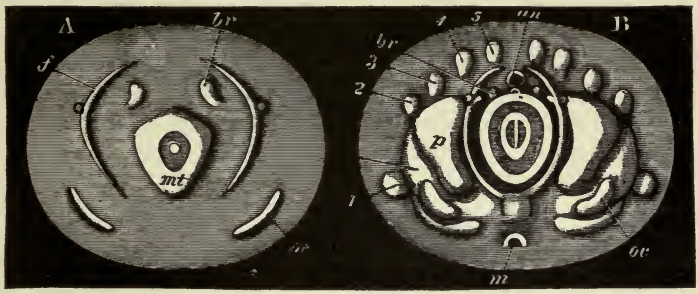


FIG. 395.—Two stages of the germinal area of *Sepia*. (From Balfour, after Kölliker.) *an*, anus; *br*, ctenidia; *f*, siphon folds; *m*, mouth; *mt*, mantle with shell gland; *oe*, eye; *p*, head lobes; *1–5* arms.

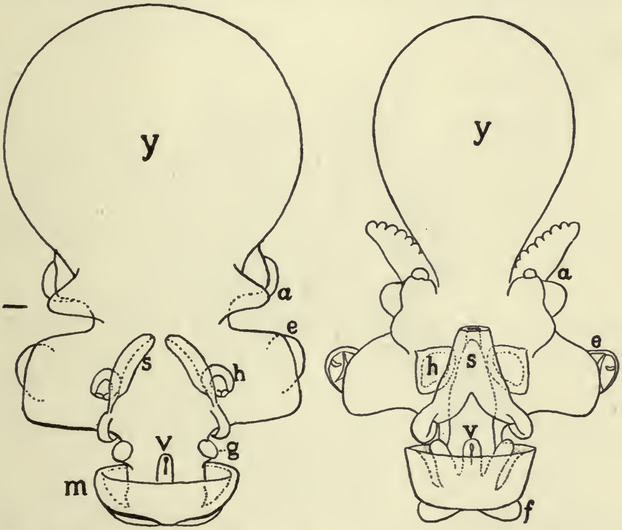


FIG. 396.—Embryos of *Loligo pealei* (orig.). *a*, arms; *e*, eyes; *f*, fin; *g*, ctenidia; *h*, otocyst; *m*, mantle; *s*, siphonal folds and siphon; *v*, anus; *y*, yolk sac.

shell gland) as flattened projections beside each other (fig. 395). Later the embryonic body becomes distinct from the yolk, which, enclosed in a cellular envelope, remains attached to the rest, near the mouth, until its substance is absorbed in the growth of the young and the animal is ready for hatching (fig. 396).

The Cephalopoda are exclusively marine. Some inhabit rocky shores, others the high seas. All are carnivorous and in turn are preyed upon by fishes, etc. Classification is based upon the number of gills and number and character of the arms.

Order I. Tetrabranchia.

With four gills, four auricles, and four nephridia; numerous tentacles without suckers, a well-developed chambered shell, siphon of two separate parapodia, and simple eyes (fig. 384). Only four living species known, all belonging to the genus *Nautilus*. The animals, which live in the Malaysian regions, are rare, but their shells are abundantly cast up by the sea. In past time the tetrabranchs were very abundant. The NAUTILIDÆ, with straight (*Orthoceras*) or coiled shells (*Goniatites*, etc.) flourished in paleozoic times. They had simple septa. The AMMONITIDÆ with folded septa were largely mesozoic. Since no living forms exist, their pertinence to the tetrabranchiates is assumed from the character of the shell.

Order II. Dibranchia.

With two nephridia, two gills, and two auricles; eight or ten arms with suckers; highly organized eyes; shell rudimentary or absent.

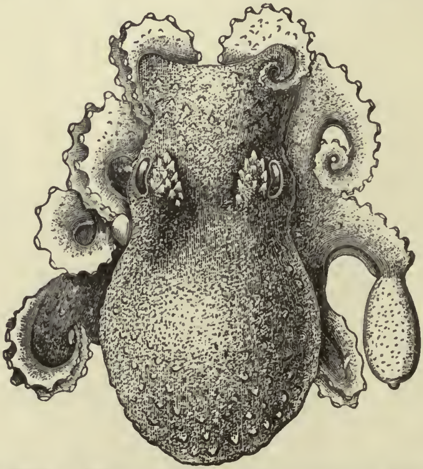


FIG. 397.—*Octopus bairdii.** (From Verrill.) A hectocotylised arm on the right side.

Sub Order I. DECAPODA. Ten arms, with lateral fins to the body. Shell usually present. SPIRULIDÆ, with internal chambered loose-coiled shell. *Spirula* (fig. 387). OIGOPSIDA, pelagic, with perforated cornea (p. 385) and two oviducts. *Ommastrephes* common in New England; *Architeuthis*,* the giant squid (p. 384). Myopsida. Oviduct single (left); cornea unperforated. *Loligo*,* common squid; *Rossia*; Sepia*, cuttle fish, furnishing the 'cuttle bone' once used in medicine, now fed to cage birds, and the pigment sepia.

Sub Order II. OCTOPODA. Eight arms webbed at their base; shell very rudimentary, sometimes fragmentary or wanting; oviducts paired, Octopodidæ, *Octopus* * (fig. 397), *Alloposus*.* Argonautidæ, female with boat-like shell (fig. 398), males much smaller and without shell. *Argonauta argo*, paper nautilus. In the Argonautidæ and Philonexidæ the hectocotylus separates of itself.

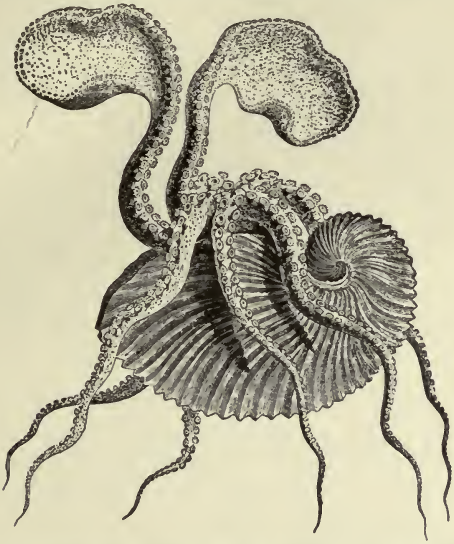


Fig. 398.—*Argonauta argo*, paper sailor, female. (After Rymer Jones.)

Summary of Important Facts.

1. The MOLLUSCA are parenchymatous animals with reduced cœlom. They consist of head, visceral sac, mantle, and foot.
2. The head bears eyes and tentacles.
3. The foot is an unpaired muscular mass used in locomotion.
4. The mantle bounds the mantle cavity which is connected with respiration; it either functions as a lung or covers the gills (ctenidia). It secretes the shell from its outer surface.
5. Foot, head, mantle, and with the latter the shell, may be lost in many groups.
6. The molluscs, without exception, agree in the nervous system.

7. Three pairs of ganglia with which three pairs of sense organs are connected almost always occur: *a*, cerebral ganglia and eyes; *b*, pedal ganglia and otocysts; *c*, visceral ganglia and osphradia (olfactory).

8. The heart is dorsal and arterial; it is enclosed in a pericardium (reduced cœlom) which connects with the nephridia by nephrostomes.

9. There is always a single ventricle and, according to the number of respiratory organs, one, two, or four auricles.

10. The alimentary canal is well developed; the liver large; salivary glands usually present. In most there is a pharynx or buccal mass with radula and jaws.

11. A veliger stage is common in development.

12. The Mollusca are divided according to the respiratory organs and appendages of the body into five classes: (1) Amphineura; (2) Acephala; (3) Scaphopoda; (4) Gasteropoda; (5) Cephalopoda.

13. The AMPHINEURA have an extremely simple nervous system in which the three pairs of typical ganglia are replaced by nerve tracts.

14. The ACEPHALA, or Lamellibranchia, lack head and cephalic appendages.

15. They are bilaterally symmetrical and have paired organs: mantle folds, bivalve shell, nephridia, and gonads.

16. In many Acephala (*Asiphonia*) the mantle folds are completely separated ventrally.

17. In the *Siphonata* the lower edges of the mantle are united, leaving three openings: (1) in front for the foot; (2) behind and below, the branchial siphon for the ingress of water and nourishment; (3) behind and above, the anal or excurrent siphon for the water used by the gills and the fæces.

18. There are two pairs of gills, which may be comb-like (true ctenidia), filiform, or most commonly lamellar.

19. Correspondingly the heart has two auricles; the unpaired ventricle is usually traversed by the rectum.

20. The foot is a compressed muscular mass frequently provided with a byssus gland.

21. The shell consists of cuticular, prismatic layer and nacreous layer. It is closed by two adductors and opened by an elastic ligament.

22. Some Acephals (*Protoconcha*) are very primitive in their gill and hinge structure; others (*Heteroconcha*) are more highly developed.

23. The SCAPHOPODA are primitive forms with tubular shells.

24. The GASTEROPODA (Cephalophora, or snails) have a distinct head bearing eyes and tentacles; a creeping foot, an unpaired mantle (occasionally absent), and a univalve shell.

25. The mantle cavity contains one or less frequently two ctenidia, or these may be degenerate and a lung may occur.

26. Nephridia and auricles are rarely paired (with paired gills); the gonads, always unpaired, are hermaphroditic or diœcious.

27. The shell is always unpaired; it is usually coiled in a (right-hand) spiral, and is frequently closed with an operculum.

28. According to characters derived from nervous system, sexual organs, heart, and respiratory organs the Gasteropods are divided into (1) Prosobranchia; (2) Opisthobranchia; and (3) Pulmonata.

29. The *Opisthobranchia* are hermaphroditic; orthoneurous; have gills of various kinds (or none), and have the auricle always behind the ventricle; shell and mantle reduced or absent.

30. The Pteropoda are pelagic Opisthobranchs with wing-like processes of the foot and frequently reduced shell or none.

31. The *Prosobranchia* have the gills (ctenidia—occasionally paired) far in front, and in consequence the auricle in front of the ventricle; they are streptoneurous and diœcious; the mantle and shell well developed.

32. The Heteropoda are pelagic Prosobranchia with foot divided into fin and tail, shell rudimentary, or naked.

33. The *Pulmonata* are in some respects (orthoneurous and hermaphroditic) Opisthobranch-like; in other respects—as in position of heart, development of shell and mantle—like the Prosobranchs; the mantle cavity functions as a lung.

34. The CEPHALOPODA have no true foot; but its homologues are to found in the siphon and in the tentacles, usually provided with suckers, on the head; they have an unpaired mantle and a single shell or none.

35. The unpaired mantle cavity contains one or two pairs of ctenidia. The water is forced from the mantle cavity through the siphon.

36. The number of auricles corresponds with the number of ctenidia; besides the systemic heart there are one or two pairs of branchial hearts, elsewhere unknown in molluscs.

37. The sexes are separate.

38. The ink sac is peculiar to Cephalopoda.

39. The eye is (usually) highly developed (with retina, choroid,

iris, cornea, vitreous body, and lens), as is the nervous system, which has, in addition to the usual centres, optic, sympathetic, and stellate ganglia.

40. The eggs have a discoidal segmentation.

41. The Cephalopoda are divided into Tetrabranchia and Dibranchia.

42. The *Tetrabranchia* (extinct save for *Nautilus*) have four gills, a chambered shell, primitive eyes, and finger-like cephalic lobes in place of tentacles.

43. The *Dibranchia* have two gills, eight or ten tentacles with suckers, and the shell is reduced or absent.

PHYLUM VII. ARTHROPODA.

Under the term Arthropoda are included the spiders, crabs, insects, and myriapods, which, together with the annelids, were united by Cuvier to form his sub-kingdom Articulata. Annelids and arthropods agree in many features. They are, as the term articulates implies, segmented animals, and they differ from the vertebrates, which are also segmented, in the extension of the segmentation, the ringing of the body, to the external surface. The boundaries between the successive segments, which cannot be recognized in the skin of the fish or other vertebrate, are marked in the articulates by a constriction of the body wall, whence the old names ἔντομα, Insecta, applied to these forms. The articulates are further characterized by a ladder-like nervous system in which the brain, present in most invertebrates, is supplemented by a ventral chain composed of ganglia metamerically arranged. The most evident distinctions between the annelids and the arthropods are (1) the character of the segmentation and (2) the presence of jointed appendages.

In superficial appearance the lines between the segments are constricted more deeply in the arthropods than in the annelids. The cause of this lies in the character of the integument (fig. 25, *f*), which is developed as a hard armor, in which two layers are recognizable, the epidermis (often called hypodermis) and the chitinous layer. The epidermis is a thin cubical or pavement epithelium, while the chitinous layer is of greater thickness and, since it is secreted by the epidermis, is stratified parallel to the surface. Its firmness is due to the chitin, which is unlike most organic substances in its resistance to acids and alkalis; only under the action of sulphuric acid and heat is it broken up into sugar and ammonia.

A firm chitinous armor would render the animal incapable of motion were there not joints between the parts. While the segments themselves are heavily armored, the cuticle between them is reduced to a delicate articular skin, and this is so protected by a kind of telescoping of the segments that injury in these softer regions is nearly impossible (fig. 399).

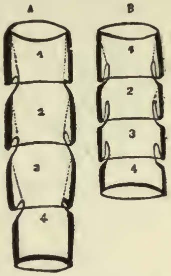


Fig. 399.—Diagram of Arthropod jointing; *A*, in expanded, *B*, in contracted condition; *1–4*, rings with connecting membranes, the muscles indicated by dotted lines. (After Graber.)

Since the ringing of the body is connected with this armoring, it disappears with the need for such protection. The hermit crabs (fig. 480) are instructive illustrations of this. These animals live with the abdomen inserted in a snail shell. That part of the body which projects from the shell is armored, while the abdomen is soft-skinned and without traces of external ringing.

The hardened cuticula causes the periodic molting (ecdysis or exuviation). When once hardened it is incapable of distension and so would prevent farther growth. Hence when the body has completely filled the armor, the latter splits in definite places and the animal crawls out of the old 'skin' (exuvia) and rapidly increases in size while the new cuticula is yet soft and extensible.

Another result of the cuticula is seen in the peculiar relations of both ordinary and sense hairs. These are cuticular structures, each usually secreted by a single epidermal cell and renewed after each molt. Each hair has a ball-like head situate in a socket in the surrounding chitin, and hence is movable; it is traversed by a canal in which is a process of the underlying matrix cell. In the case of sensory hairs these structures are connected with a nerve (fig. 77). The sense cell, like a bipolar ganglion cell, has two processes; one peripheral, which enters the axis of the hair, the other central, which runs as a nerve fibre to the central nervous system. The cell itself may be in the epithelium or situated deeper and interpolated as a ganglion cell in the sensory nerve.

Another important character is the heteronomous segmentation, which, in the lowest forms (*Peripatus* and Myriapods), is little pronounced, but elsewhere leads to a marked inequality of the divisions of the body and to a greater centralization of structure. Different body regions may be distinguished. A few segments at the anterior end always fuse and form a head (fig. 400, *C*); behind this there is usually a second segment complex, the thorax (*T*), and then a third, the abdomen (*A*). An apparent reduction of regions can occur when the head and thorax unite (fig. 401, *Ct*) to form a cephalothorax; or again the number of regions may be increased (fig. 402) by a division of the abdomen into abdomen proper (*A*)

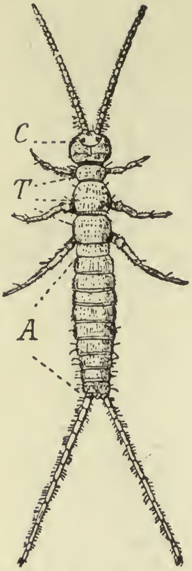


FIG. 400.

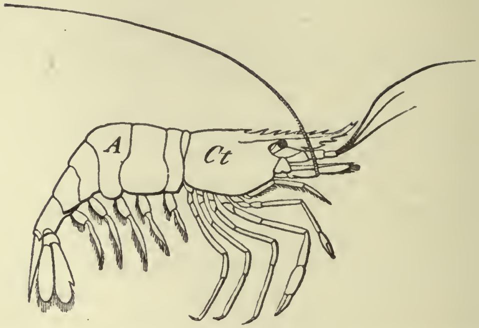


FIG. 401.

FIG. 400.—*Campodea staphylinus.* (From Huxley.) *A*, abdomen; *C*, head; *T*, thorax.
FIG. 401.—*Palœmon serratus.* (From Ludwig-Leunis.) *A*, abdomen; *Ct*, cephalothorax.

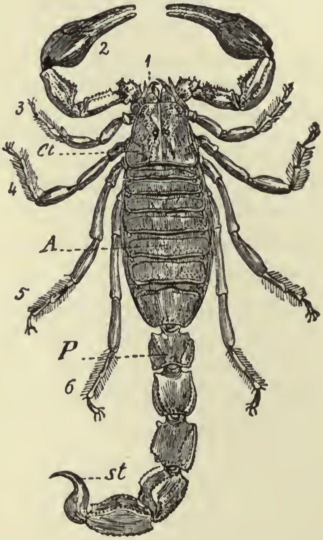


FIG. 402.

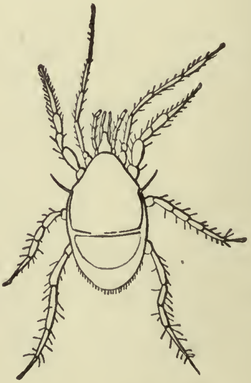


FIG. 403.

FIG. 402.—*Androctonus australis.* (From Blanchard.) *A*, abdomen; *Ct*, cephalothorax; *P*, post-abdomen; *1*, cheliceræ; *2*, pedipalpi; *3–6*, legs.
FIG. 403.—*Gamasus coleoptratorum.* (From Taschenberg.)

and post-abdomen (*P*). Finally, in many arthropods (*e.g.*, the mites or acarina, fig. 403) it is impossible to recognize regions or somites because internal fusion of parts has obliterated the external evidences of segmentation.

In order clearly to understand what is meant by head, thorax, etc., requires a consideration of the second character distinguishing the arthropods from the annelids, the jointed appendages, which give the name to the former group. The arthropodan appendages are highly developed parapodia, differing in being jointed to the body, in consisting of a series of joints themselves, and in having their intrinsic musculature. As was first pointed out by Savigny, there is but a pair of appendages to a somite, and this belongs to the ventral surface. Hence it follows (Savigny's law) that if any region shows no external signs of segmentation, but bears more than one pair of appendages, we conclude that the region is a complex of at least as many somites as there are pairs of appendages. Thus the unsegmented head of an insect consists of four somites, the cephalothorax of a lobster of thirteen, for the one bears four, the other thirteen, pairs of appendages. Ontogeny supports this, for in the embryo the somites are clearly visible.* It is not necessary that each somite in the adult should bear appendages, since these may disappear in growth without leaving a trace.

The appendages subserve many functions (fig. 404). Their primary purpose is locomotion. Locomotor appendages (*pereiopoda*, feet or legs) are long and consist of a number of well-developed joints which may form flattened oars or may be provided with claws for creeping (*8*). Besides locomotor appendages there are tactile appendages or antennæ (*1*), chewing appendages (jaws, mandibles, maxillæ, *2–4*), false feet or pleopoda (*9*) of varying functions, and forms—maxillipeds (*5–7*)—transitional between jaws and legs.

Aside from their tactile function, antennæ are characterized by position and innervation. They are always placed in front of the mouth and receive their nerve supply from the supraœsophageal ganglion, while all other appendages are innervated from the ventral chain.

The form of the jaws is strikingly modified. One or two basal joints serve for the comminution of food, and these parts are strong and are covered especially on the medial side with a hard, toothed chitin (figs. 404, *2*; 410, *II*, *V*; 507). The other joints may entirely disappear. When they persist they form a more or less leg-like appendage, the palpus. Since several appendages may be modified into jaws, the first are called mandibles, the next maxillæ, and second maxillæ may follow. The maxillipeds may have more the appearance of jaws, at other times are more leg-like (fig. 404, *5–7*).

---

* This statement is not exactly correct, for in certain insects and in the lobster there is one somite which is entirely lost in the adult.

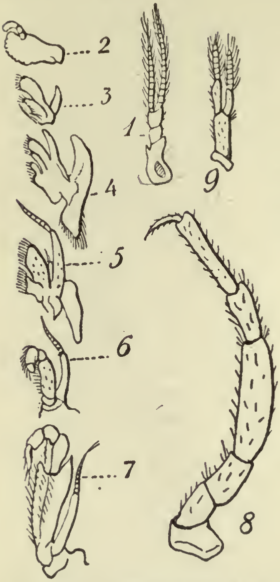


FIG. 404.—Appendages of the crayfish. *1*, first antenna; *2*, mandible; *3*. *4*, first and second maxillæ; *5*, *6*, *7*, maxillipeds; *8*, walking leg; *9*, pleopod.

The false feet (pleopoda) are small and inconspicuous appendages which may have various functions: they may serve as gills or supports for the gills, as places for the attachment of eggs, as organs for the transfer of sperm, or as swimming or creeping organs.

These appendages have constant positions in the body. First on the head come the antennæ and then, in the region of the mouth, the jaws and, so far as they are present, the maxillipeds. Third come the true feet, and lastly, when they exist, the false feet. Those somites which bear antennæ or jaws belong to the head, those bearing walking feet to the thorax, while the somites of the abdomen bear either false feet or lack appendages. As a sequence the cephalothorax is that region of the body which bears, besides antennæ and jaws, legs as well.

The extremities of Arthropoda have given rise to various disputes. Many zoologists speak of a pre-antennal somite and a pre-antennal appendage, referring to the eye stalk of a part of the Crustacea, which, however, differs markedly in its development from the true appendages. Those who accept an ocular somite must add one to the number of somites as stated in this volume. A second theory regards the antennæ as ventral appendages innervated from the ventral chain which secondarily become dorsal and receive their nerves from the brain. This view is firmly grounded for the second antennæ of the Crustacea. Other questions are as to the possible loss of segments and appendages.

The concentration or fusion of somites to body regions has had an influence upon the internal structure and especially upon the nervous system (fig. 405). A ladder-like nervous system consists, as was pointed out (p. 124), of a dorsal brain (supraœsophageal ganglia) and a ventral chain of ganglia, all connected by longitudinal nerve cords, the brain being connected with the rest by cords or commissures passing on either side of the œsophagus. The ventral chain should contain as many pairs of ganglia as there are somites, but this is not the case except in the embryo. The tendency is rather towards a fusion of ganglia, especially of those somites which unite or fuse. This fusion of ganglia occurs to a varying extent in different species, the extreme being reached in the spiders and crabs (fig. 441), where the whole ventral chain forms a large ganglionic mass. In all cases, however, the brain remains distinct from the rest, its position dorsal to the œsophagus precluding its fusion with the ventral chain.

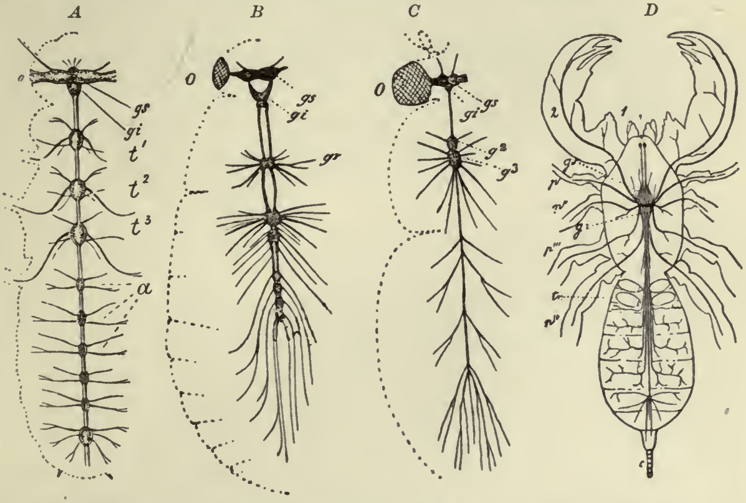


Fig. 405.—Different degrees of concentration of the ventral cord of Arthropods. (From Gegenbaur.) *A*, Termite (after Lespès); *B*, water beetle (after Blanchard); *C*, fly (after Blanchard); *D*, Thelyphonid (after Blanchard). *a*, abdomen; g^2, g^3, ganglia of ventral cord; *gi*, infraœsophageal ganglion; *gs*, supraœsophageal ganglion; *o*, eye; p'-p'^{v}, walking feet; *tr*, lung books; *1*, cheliceræ; *2*, pedipalpus.

Of the sense organs the best known are the eyes, of which two types are recognized, the simple (ocellus, stemma) and the compound (faceted). The ocelli are very small. In their highest development, as in spiders (fig. 406), they are composed of lens, vitreous body, and retina. The lens is formed by the cuticula, the rest from the epidermis. The lens differs from the rest of the cuticle in being transparent, and is usually thickened to a biconcave body (*1*) which converges the light upon the retina. Behind the lens comes a layer of transparent cells, the vitreous body (*2*), and behind this, in turn, the retina, consisting of cells which, at the one end, bear 'rods' (*4* and *7*), at the other pass into nerve fibres. The retina and vitreous body, surrounded by pigment, form a spherical thickening sharply marked off from the rest of the epithelium. These eyes, like those of vertebrates, must form inverted images.

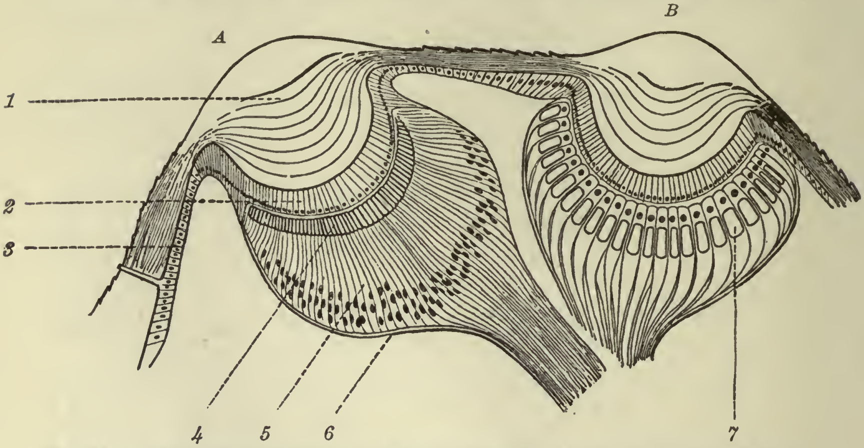


FIG. 406.—Diagrammatic section through anterior (*A*) and posterior (*B*) eyes of *Epeira diademata*. (After Grenacher.) The hinder eye shows the inverted retina; *1*, lens; *2*, vitreous body; *3*, epidermis, outside this, chitinous layer; *4*, rhabdomes; *5*, retinal cells; *6*, capsule of eye; *7*, rhabdomes of inverted eye.

In many spider eyes there is an inversion recalling that of the vertebrates (fig. 406, *B*), the rhabdome lying behind the nuclear portion of the cell. Behind the rhabdomes comes a layer of strongly iridescent cells, the tapetum lucidum.

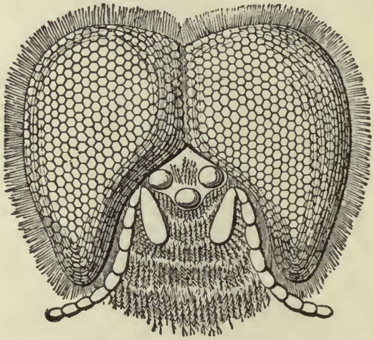


FIG. 407.—Head of drone bee (After Swammerdam, from Hatschek.) Showing the large faceted eyes and between them three ocelli.

The compound eyes are much larger. They owe their name 'faceted eyes' to the fact that the cuticle over them is divided into polygonal (usually hexagonal) areas or facets (fig. 407). Each facet corresponds to a small chitinous lens (the number of which varies, in different species, between a dozen and several thousand),

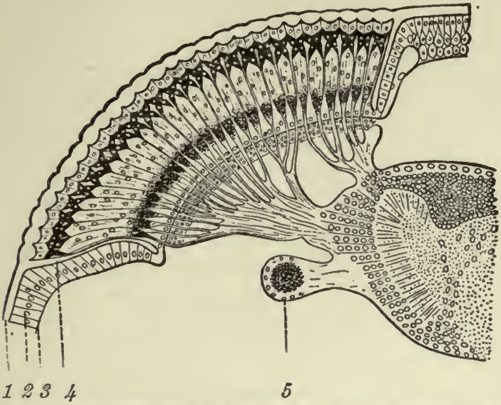


FIG. 408.—Section of compound eye of *Forficula*. (After Carrière, from Hatschek.) *1*, cuticula, producing the cornea of many lenses over the eye; *2*, epidermis, which in the eye forms the ommatidia; *3*, basal membrane; *4*, reentrant chitinous fold ('sclerotic'); *5*, rudimentary larval eye.

and bounds the eye externally, whence this layer is called the cornea (fig. 408). The part of the eye beneath the cornea consists of radially arranged prismatic parts or *ommatidia* which correspond in number and position to the facets, their broader ends being placed beneath the facets, their narrower internal ends connecting with fibres of the optic nerve which go to the brain. Each ommatidium (fig. 409) has essentially the structure of an ocellus: (1) the lens (*l*) with its epithelium; (2) the vitreous body (*kz*); (3) the retinula (*rz*). The vitreous body is usually composed of four cells which in the so-called euconous eyes surround a transparent body, the crystalline cone (*k*), secreted by these cells. The retinular cells are almost always seven in number, each bearing on its inner surface a rhabdome (*r*), the seven rhabdomes frequently fusing into a common mass. Each ommatidium is surrounded by a pigment sheath, isolating it optically from its fellows.

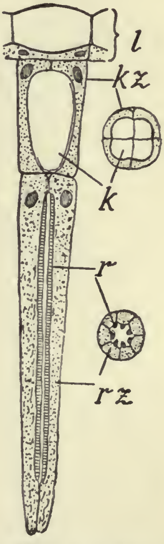


FIG. 409.—A single ommatidium (with sections) of a compound eye. *k*, crystalline cone; *kz*, cone cells; *l*, lens with hypodermis; *r*, rhabdomes; *rz*, retinular cell.

From this it appears that the compound eye may be regarded as a complex of ocelli. This anatomical conception must not, however, obscure the physiological. As Johannes Müller first pointed out, the whole compound eye forms but a single erect picture composed of separate images of small area formed by the separate ommatidia. This 'mosaic theory' has completely replaced the view that each ommatidium formed a complete inverted picture.

While the number of ocelli varies, the compound eyes are almost always two in number. Where, apparently, as in the Daphnidæ, there is but one, there is in reality a fusion. There is also constantly present a large optic ganglion where the optic nerve enters, but lying outside the eye itself.

The tactile organs, consisting of tactile hairs (fig. 77), are uniform in structure. On the other hand the senses of hearing, taste, and smell are subserved by varying organs. It is to be regretted that we know but little of these senses in arthropods, although beyond question they are frequently well developed. The sense of smell resides chiefly in the antennæ and in the palpi of the jaws. The organs are olfactory cones (modified hairs) which frequently lie in pits in the skin. Similar organs in the mouth are probably connected with taste. As organs of hearing (? equilibration) besides the otocysts of the Podophthalmata and the tympanal organs of the Orthoptera, the widely distributed 'chordotonal' nerve ends of insects are to be mentioned.

Concerning the alimentary canal it need only be said that the larger proportion of it is formed of ectodermal stomodeum and proctodeum, while the entodermal portion (mesenteron) forms on an average but one third of the total length. At ecdysis the chitinous lining of these parts, including the large chewing stomach, is cast with the rest of the integument. The entire absence of ciliated epithelium is noteworthy. Ciliated cells have never been found in arthropods.

The most constant portion of the circulatory system is the heart, which usually lies immediately beneath the back and is enclosed in a more or less distinct sac which, although called pericardium, is not a part of the cœlom. From the pericardium blood passes into the heart by openings right and left, the ostia. Since the margins of the ostia project far into the lumen of the heart and so form folds functioning as valves, the heart itself may be divided into a series of chambers, especially distinctly separated from each other by the progressive contraction of the wall (fig. 66). The chambers disappear when, with reduction of the body, the heart shrinks to a sac. In small arthropods the heart together with the whole vascular system may be lost. Since the Annelida have a well-developed circulatory system, this loss in these animals must be regarded as secondary rather than as primitive, and is explained by the fact that with reduction in size the organization is simplified.

The blood may pass from the large arteries either directly into the large blood sinuses of the body, erroneously called the body cavity, or by a more complicated course through capillaries and veins as well as through the respiratory organs. There is, on this account, the greatest difference in the development of the vascular system, but even in the highest forms the system is not entirely closed, the blood passing to the sinuses of the body (hæmocœle, p. 110) and thence to the pericardium (probably arising from the coalescence of veins and certainly not cœlomic), from which it is sucked through the ostia into the heart.

The variations in the circulation depend upon the modifications of the respiratory organs, which can be described adequately only in connexion with the various groups. In general it can only be said that the more respiration is localized in regions and organs the more nearly complete is the circulation, while with respiration diffused over or through the whole body, the vascular system, including even the heart, may be reduced.

The various spaces in the body are frequently encroached upon by a *fat body,* a kind of connective tissue whose cells, richly laden with fat, serve as a store of nourishment for the animal. Besides, urinary products, like uric acid, have been found in it, leading to the conclusion that the fat body acts as a reservoir for excretory substances before their elimination by the excretory organs. These latter vary greatly in the different groups: true nephridia in *Peripatus,* shell glands and antennal (green) glands in the crustacea, and tubules (Malpighian tubules) connected with the intestine in arachnids and insects.

The sexual organs, which empty through ducts which are apparently modified nephridia, are only rarely hermaphroditic. In the bisexual species one can usually distinguish males and females by external characters, such as coloration, size or form of appendages, especially those used in copulation. The eggs are usually large and rich in yolk, and consequently but rarely undergo total segmentation. In most eggs occurs that type of partial segmentation called superficial (fig. 104). While the surface of the egg divides into the cells which form the blastoderm, the central yolk long remains undivided—a condition of systematic interest since it is not known to occur outside the Arthropoda.

The cases of discoidal and unequal segmentation are apparently derived from the superficial.

In accordance with their high organization, reproduction by fission or budding never occurs, but parthenogenesis and pædogenesis do. In some parthenogenesis has a certain relationship to the life history. In lower crustacea and in Aphides (plant lice) it allows the species to spread rapidly in large numbers over suitable feeding grounds. Among the bees parthenogenesis has a relation to the sexes, since males are only produced from unfertilized eggs. Along with parthenogenesis—there may be rare exceptions—sexual reproduction occurs, so that not rarely asexual alternates with sexual generation (heterogony), though not in such a pronounced manner as in the worms.

The French entomologist Latreille divided the Arthropods into four classes: Crustacea, Myriapoda, Arachnida, and Insecta. Later the discovery, by Moseley, that *Peripatus* possesses tracheæ led to the creation of a new class, Protracheata, and the grouping of all arthropods into branchiate and tracheate divisions, the branchiates including the crustacea alone. Later researches have shown that these divisions are not natural and that tracheæ have had different origins, the spiders being nearer to the crustacea than to the insects, and that crustacea and insecta have come from the annelids through different lines. Similarly the myriapods have been divided, one group, the chilopods, being closely related to the true insects, the other (diplopods) being very uncertain in position.

Class I. Crustacea.

The Crustacea owe their name to the fact that their chitinous cuticle is usually rendered hard and firm by deposits of carbonate and phosphate of lime and, in contrast to that of other arthropods, has lost much of its elasticity and has become 'crusty.' Another important characteristic is the habitat of the group; the Crustacea are typically aquatic and hence breathe by means of gills. This branchial respiration persists, as in the case of crayfish, when the animals are taken from the water, for they retain water in the gill chamber and hence for a long time the gills are wet by this fluid. There are but few exceptions to this rule, as some land crabs and the sow bugs; these breathe air, either by means of the gills or by special structures in the gill chamber to be mentioned later.

The branchiæ or gills are always placed where a rapid exchange of water is possible. The appendages afford such a position, and hence one finds the gills as thin-skinned vascular plumes or plates (figs. 61, 437) either on the appendages or on the body near by, or the whole appendage may take a leaf-like, thin-skinned shape and thus serve as a gill (figs. 411, 451). Besides, the whole body surface may be respiratory and in small forms may entirely replace that of the gills, so that these organs become rudimentary or may entirely disappear, there being a diffuse respiration with corresponding results in the circulatory system. With a localized respiration heart, arteries, capillaries, and veins are well developed, but with the diffuse respiration only the heart persists as a reduced structure, or with its disappearance the last traces of a circulatory system are lost.

Locomotion as well as respiration is related to the aquatic life, and these animals usually possess a special form of appendage of the biramous or *schizopodal* type, which at once differentiates these forms from other arthropods. While in the latter, as every insect shows, the joints of the limb follow in a single sequence, the crustacean appendage has a two-jointed base (basiopodite), followed by two many-jointed branches (fig. 410, *I*), an inner or *endopodite* and an outer or *exopodite*.

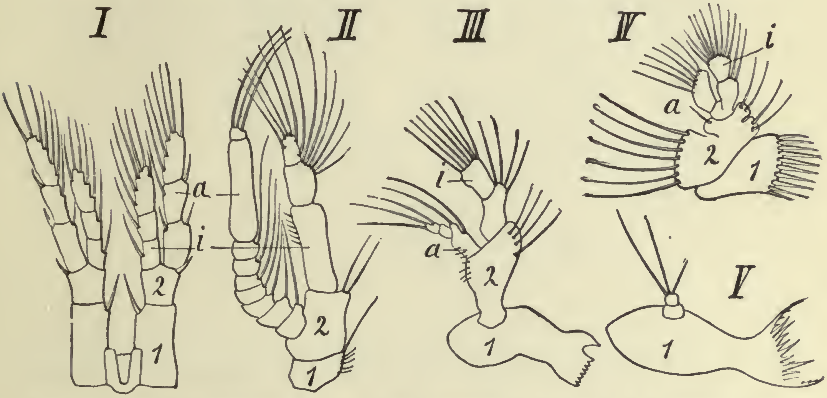


Fig. 410.—Copepod appendages. *I-IV, Diaptomus castor; I*, a pair of schizopodal feet; *II*, second right antenna; *III*, right mandible; *IV*, right maxilla; *V*, right mandible of *Cyclops coronatus*. *1, 2*, joints of basiopodite; *i*, endopodite; *a*, exopodite.

The schizopodal appendage occurs only when the limb is used for swimming; when it is used for walking upon the bottom, as in crayfish and crabs, the exopodite is lost and only the endopodite persists as the functional limb, which then closely resembles the appendages in the so-called tracheates. This loss rarely occurs on all the appendages; usually the abdominal feet and the mouth-parts retain the two-branched condition. Embryology further shows that even in the case of the crabs all the feet are at first schizopodal and that the walking legs lose the exopodite during growth. There is some evidence to show that the schizopodal foot is not the primitive type. This is furnished by the phyllopod foot (fig. 411, *II*), and consists of a medial axis, *b*, bearing on the inside six 'endites,' *i*, and on the outer side two 'exites,' a flabellum or epipodite, *a*, and a gill, *k*.

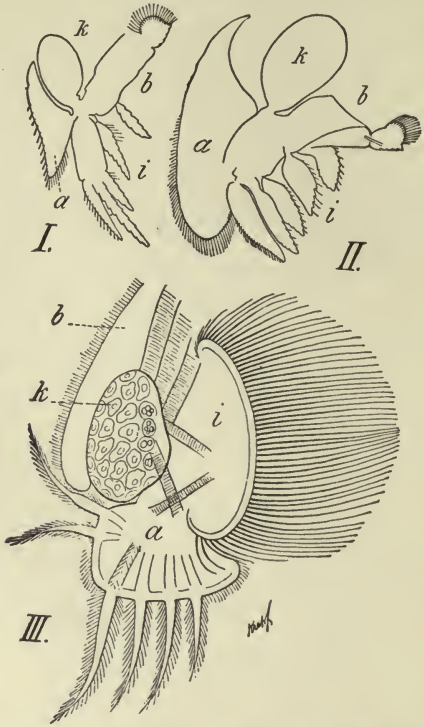


Fig. 411.—Branchiopod appendages. *I* and *II* first and sixth legs of *Branchipus grubei* (after Gerstäcker); *III*, fourth leg of *Daphnia simus* (after Claus). *a*, flabellum; *h*, basis; *i*, axon and its endites; *k*, gills.

This becomes modified into the schizopodal form by a loss of the four basal endites (those nearest *b*) and the development of the two terminal endites into exopodite and endopodite. Still the schizopodal condition is so nearly universal among Crustacea that it must be accorded great weight in classification.

The appendages furnish a further diagnostic character in that two pairs of antennæ are present in the crustacea (see, however, Trilobitæ). Antennæ, it will be remembered, are preoral appendages innervated from the brain. In some cases, as many Entomostraca, the second pair may lose their sensory functions and become mere swimming organs.

A carapace, recalling the mantle of the molluscs, is widely distributed in the crustacea. It arises as a fold from the head, which may extend backwards as a shield, completely covering some or all of the thoracic segments (fig. 412), or it extends right and left on the sides of the body (fig. 426) and produces two valves strikingly like those of a lamellibranch, the resemblance being strengthened in the cirripeds and ostracodes by the extensive calcification.

Concerning the internal organs but few general remarks can be made. Salivary glands are wholly absent; on the other hand the stomodeum is usually widened into a strong chewing 'stomach,' and behind this empty the ducts of the so-called liver (better hepato-pancreas). The liver itself differs widely from the two simple blind sacs of the Daphnidæ (fig. 420) to the enormous livers of the Decapoda (fig. 439, *A*). Excretory organs are represented by so-called *green glands* (antennal glands) and *shell glands*. The latter, which received their name from the erroneous idea that they produced the shell, open to the exterior on either side at the bases of the fourth appendages, the maxillæ (fig. 420, *s*). The green gland opens similarly on the basis of the second antennæ. Both have essentially the same structure (fig. 413); they begin with a terminal vesicle (in the case of the antennal gland in close relations with the reduced cœlom), which passes into a slender, greatly coiled tube. Their structure and development lead to the conclusion that they are modified segmental organs. Both occur

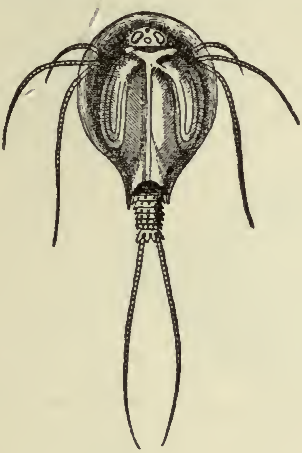


FIG. 412.

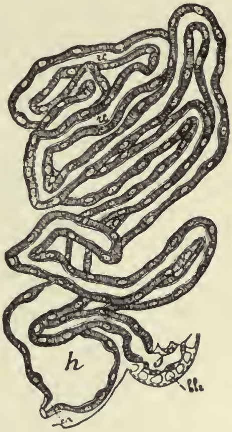


FIG. 413.

FIG 412.—*Apus cancriformis.* (After Ludwig-Leunis.) The segments mostly covered by the carapace.
FIG. 413.—Antennal gland of *Mysis*. (After Grobben.) *blr*, blood lacunæ; *ea*, external opening; *h*, bladder; *rc*, canal; *s*, internal vesicle.

together only in the larvæ; in the adult one or the other is suppressed. In some amphipods there are excretory diverticula developed from the intestine (fig. 448), which resemble the Malpighian tubes of insects, but differ from them in being of entodermal origin. In some decapods cæca occur in the same region, but nothing is known of their function.

Visual organs are either represented by the so-called *nauplius eye,* consisting of a pigment spot with three lenses situated directly on the brain, or by a pair of compound eyes. The nauplius eyes are chiefly found in the lower, the compound in the higher, groups; occasionally they coexist in the same species. Auditory (equilibration) organs (otocysts) occur only in the Malacostraca, either in the base of the first antennæ or in the endopodite of the last abdominal feet (fig. 434, *o*). These are rarely vesicular, but are usually grooves (fig. 414), bearing at the base a row of chitinous sense hairs, the crista acustica, connected below with an auditory nerve, while their free ends extend between a cluster of otoliths.

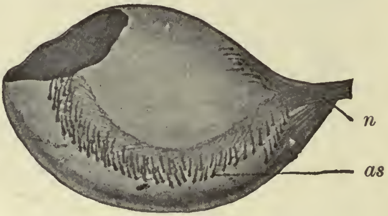


FIG. 414.—Otocyst of crayfish. *as*, auditory ridge; *n*, nerve.

At ecdysis these otocysts with their sensory hairs and otoliths are cast off. If a crayfish which has just molted be placed in perfectly clean water, the otocyst will remain without otoliths; but if some easily recognizable substance, like uric acid crystals, be placed in the water, some of these will soon be found in the sac, thus proving that the otoliths are introduced from the outside.

Crustacea are only exceptionally hermaphroditic. The spermatozoa are noticeable for their great size, in many ostracodes equalling the body in length. Except in the Cirripedia the spermatozoa lack a flagellum and are immobile. Their round or elongate body is covered with rigid processes reminding one of the pseudopodia of *Actinosphærium* (fig. 36, γ, δ). They are frequently enclosed in spermatophores (fig. 422).

The typical development of a crustacean includes a metamorphosis, and where direct development occurs the metamorphosis is either suppressed or, as is easily shown, the corresponding stages are passed in the egg. Two of the larval stages are especially important, the nauplius and the zoea. The *nauplius* (figs. 7, 429) consists of three segments covered by a dorsal shield and bearing below three pairs of appendages. The first pair, developing later to the first antennæ, are simple; the others, corresponding to the second antennæ and mandibles, are schizopodal. Internally there is a three-chambered alimentary tract, a supraœsophageal ganglion on which is an unpaired eye, and a ventral chain. The nauplius is almost universal among the lower crustacea, and some writers believe that it represents an ancestral form from which the crustacea have descended, a view open to much objection.

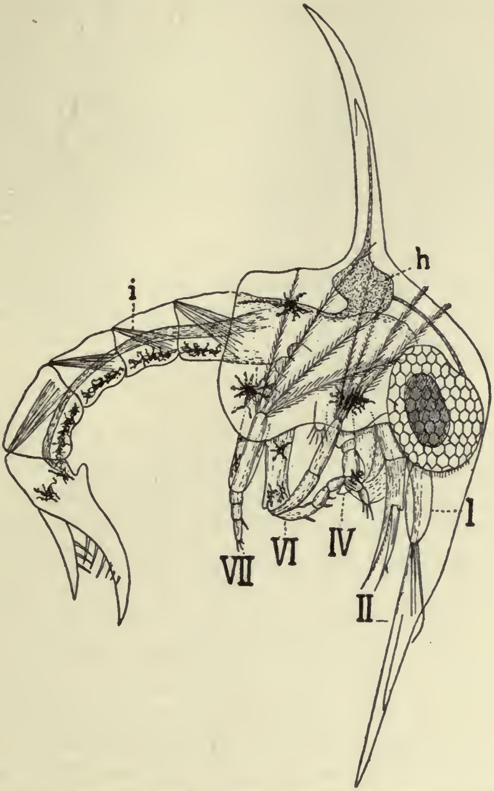


FIG. 415.—Zoea of *Carcinus mœnas.* (After Faxon.) *h*, heart; *i*, intestine; *I-VII*, cephalic appendages.

The *zoea* is more complex. It consists (fig. 415) of cephalothorax and abdomen, the latter without appendages, the former with several pairs of schizopodal swimming feet. There are two large compound eyes and, dorsal to the intestine, a heart. Frequently the carapace is armed with very long spines projecting from front, back, and sides, which are intended as protection from enemies.

Nauplius and zoea are of systematic importance, since they rarely both appear in the life cycle of one individual. The nauplius is characteristic of the lower crustacea—the 'Entomostraca.' The zoea, on the other hand, has never been noticed in the Entomostraca, but occurs in many Malacostraca. A nauplius appears in only a few Malacostraca, like the schizopods and *Peneus*, and there precedes the zoea stage. It must not be forgotten that many forms among both Entomostraca and Malacostraca have no zoeal or nauplius stage.

Frequently the lower crustacea are united under the name Entomostraca, but, aside from the nauplius stage and the possession of a shell gland, the only characters of the group are negative.

Sub Class I. Trilobitæ.

The most important fossils of the class of crustacea are the Trilobites which appeared in the Cambrian and died out in the Permian, being extremely abundant in the Silurian. The body (fig. 416) consists of head and trunk, the latter segmented. In the young the segments are very few, but increase in number with age (10–29, according to the species). The hinder segments frequently differ from the rest and form an abdomen or *pygidium*. Dorsally the animal is divided by two grooves into three lobes, marking off in the head a *glabella* and two *genæ;* in the trunk *rhachis* and two *pleuræ*. On the head there are usually a pair of compound eyes, which in the young were frequently ventral, but are brought to the dorsal surface with growth. For many years little was known of the under surface, but lately specimens of *Triarthrus becki* (fig. 417) from the Utica slate have revealed the appendages. On the head are a pair of simple antennæ, and four pairs of schizopodal feet, the bases of which acted as jaws. It is a question whether the first pair of jaw feet correspond to the second antennæ or whether these have been lost in the group. The trunk segments bear biramous feet.

In some respects the trilobites resemble the Xiphosura (*infra*), but the possession of antennæ and biramous feet place them among the crustacea. Here their position is very uncertain. We have little knowledge of but one species, and this with its single pair of antennæ differs from all recent crustacea.

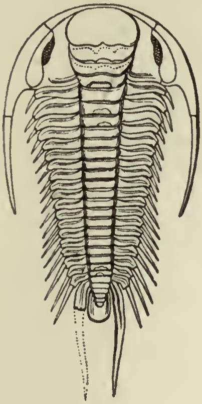


FIG. 416.

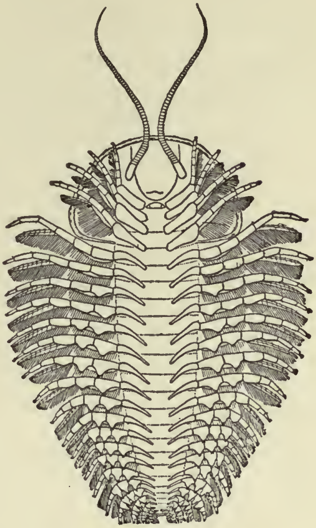


FIG. 417.

FIG. 416.—*Paradoxides bohemicus.* (From Zittel.)
FIG. 417.—*Triarthrus becki*, ventral surface, restored. (After Beecher.) The head bears one pair of antennæ and four pairs of biramous feet, the basal joints serving as maxillæ. Trunk with biramous feet.

Sub Class II. Phyllopoda.

The Phyllopoda are clearly the most primitive of crustacea. The name is derived from the leaf-like feet (p. 410), which occur upon the thoracic region. More anteriorly the appendages are schizopodal, the second pair of antennæ often being efficient swimming organs. The number of body segments varies between very wide limits, there being less than a dozen in the Cladocera, while, if Savigny's law (p. 401) holds true, there are over sixty in some Apodidæ. In most forms (the Branchipodidæ excepted) a carapace is developed by a backward growth from the head. This forms a broad oval shell covering most of the body in the Apodidæ (fig. 412); in the Estheriidæ and Cladocera it is divided into right and left halves hinged together in the mid-dorsal line, thus giving these animals the appearance of bivalve molluscs.

These forms have, besides the unpaired nauplius eye, a pair of compound eyes which in the compressed forms are frequently fused, although distinct in the young and retaining the double optic nerve throughout life. The liver is present in the shape of simple cæca; the heart, elongate, chambered, and with many ostia in the Branchiopoda, a short sac with only a pair of ostia in the Cladocera (fig. 420, *h*), lies dorsal to the intestine. The shell gland is well developed.

In development summer and winter eggs are distinguished. The summer eggs form a single polar globule and develop parthenogenetically. The winter eggs form two polar globules and require fertilization. The thin-shelled summer eggs are carried about by the mother in a brood pouch and hatch in a relatively short time. The thick-shelled winter eggs are cast off and fall to the bottom, where they require a long time for development. They may be dried or frozen without injury, and at least in some cases drying is necessary to their development. This feature explains the appearance in early spring of large numbers of *Branchipus* and *Estheria* in snow pools which are dry throughout the summer. On our western plains and in Europe *Apus* occurs in the same way. These peculiarities of reproduction are readily understood when we recollect that the phyllopods are largely inhabitants of fresh water. The winter eggs preserve the species through times of drought and cold; the summer eggs are for the rapid increase of the species during the wet season. The same relations also explain the fact that males are rare and only appear at intervals, indeed are not known in many species.

Order I. Branchiopoda.

The Branchiopoda are relatively large with numerous segments, leaf-like appendages, long, chambered heart, and lack swimming antennæ. With few exceptions they are inhabitants of fresh water. According to the development of the carapace they are subdivided into three families.

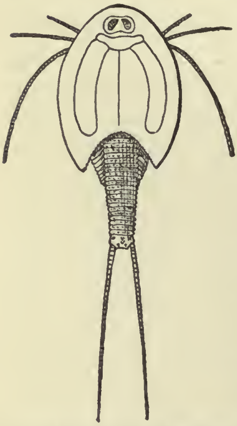


Fig. 418.—*Apus equalis*.* (After Packard.)

1. Apodidæ. Body depressed, with large oval undivided carapace. Eggs carried in brood capsules formed by a pair of appendages. *Apus* (fig. 412) and *Lepidurus* occur in Europe, Greenland, and the United States west of the Missouri. *Protocaris* of the Cambrian rocks is apparently an Apodid.

2. Branchipidæ. Body without carapace, the second antennæ of the male large and modified into an organ for clasping the female. The female carries the summer eggs in a wide 'uterus' in the abdomen. *Branchipus* lives in fresh water, *Artemia* in brine, and in certain species one has been transformed into the other by changing the water from fresh to salt or the reverse. *Branchipus vernalis* (fig. 419) occurs in snow-water pools in our northern states, *Artemia* in Great Salt Lake, around salt works or in tubs of brine near the ocean.

3. Estheriidæ. Body laterally compressed and enclosed in a bivalve shell, compound eyes fused; male very rare. *Estheria*,* *Limnadia*,* in fresh water.

Order II. Cladocera.

Like the estheriids the small Cladocera have the body enclosed in a bivalve carapace, which, in some instances, is small and reaches back only over the first trunk segments, in others is large, enclosing the body, with a notch for the protrusion of the head, while behind it terminates in a sharp spine. The head bears a pair of large swimming antennæ and a much smaller first pair bearing olfactory bristles and, in the male, hooks for clasping the female. The body consists of few segments, the heart is a simple sac, and the fused faceted eyes, with paired optic nerves, are capable of motion in a special optic capsule.

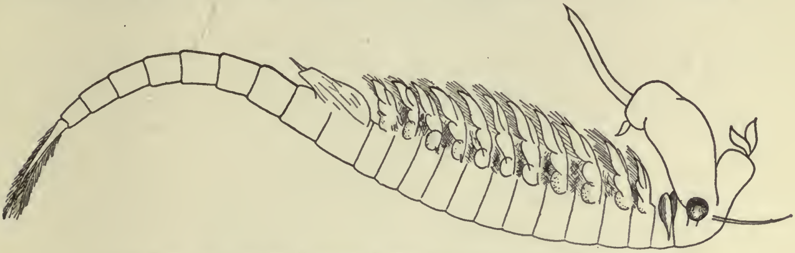


Fig. 419.—*Branchipus vernalis*,* fairy shrimp. (After Packard.)

The young eggs in the sexual organs always occur in groups of four (fig. 420). Of these but one grows into an egg, the others breaking down and serving this as nourishment. Larger eggs with more yolk occur when several of these groups (2–12 fuse to form a single egg. The summer eggs arise from a single group, the winter eggs from several groups of primordial ova.

In all Cladocera the space between the back of the animal and the shell serves as a brood pouch. In some cases this pouch contains an albuminous fluid secreted by the mother, which nourishes the embryo. The larger winter eggs—one or two in number—frequently remain for awhile in the brood chamber and are there enveloped in a peculiar shell, the ephippium, consisting of two chitinous plates, like watch crystals, their edges closely appressed.

Daphnidæ. Shell well developed; *Daphnia** (fig. 420), *Bosmina*.* Polyphemidæ. Shell small, only functioning as a brood case; head with an enormous eye and large swimming antenna; no phyllopodous feet; marine and lacustrine. *Leptodora hyalina** appears at night, sometimes in great numbers, in some of our lakes. *Evadne*,* marine.

Sub Class III. Copepoda.

A general description of the copepods can only apply to the non-parasitic forms, since many of the parasites have become so

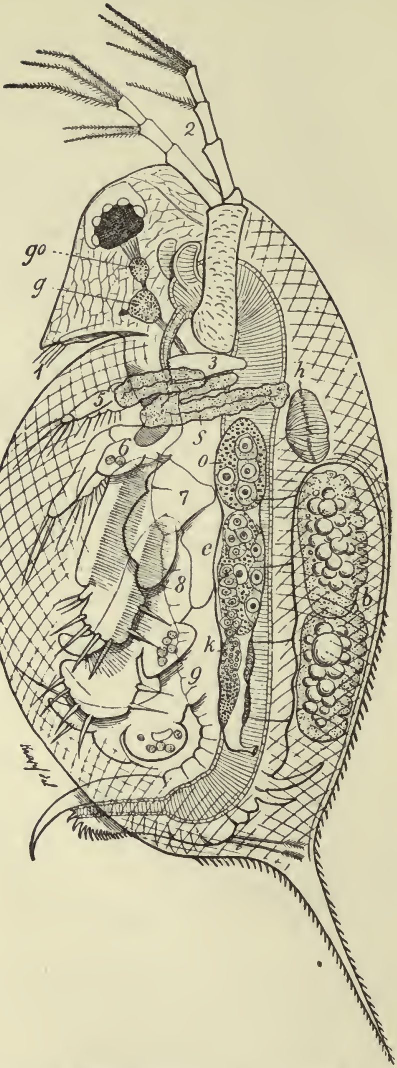


FIG. 420.—*Daphnia pulex.* *b*, brood chambers with embryos; *g*, brain with nauplius eye; *go*, optic ganglion; *h*, heart; *o*, ovary; *s*, shell gland. The eggs arise at *k*, and separate, forming in groups of four, as at *e*, of which one becomes the egg, while the others abort (*o*) and form food. The egg then passes to the brood chamber. *1*, *2*, first and second antennæ; *3*, mandible (maxilla rudimentary and invisible); *5–9*, legs. *g*, brain; *go*, optic ganglion; *h*, heart.

degenerate (figs. 6, 423) as to be recognized even as arthropods only by a knowledge of the development. The sixteen somites of the body are nearly equally divided among the three regions—

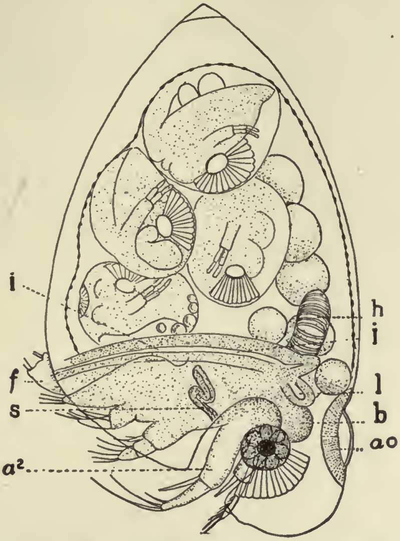


Fig. 421.—*Evadne* (orig.), showing the brood pouch filled with eggs and young. a^2, second antenna; *ao*, adhesive organ; *b*, brain; *f*, furca; *h*, heart; *i*, intestine; *l*, liver; *s*, shell gland.

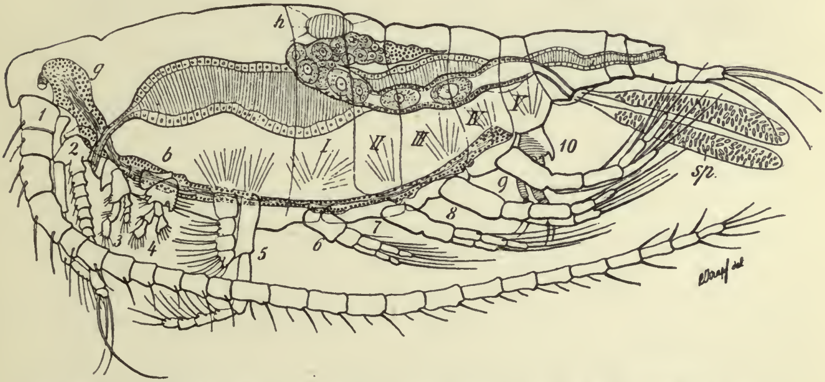


Fig. 422.—*Diaptomus castor*. *b*, ventral nerve cord; *g*, brain with nauplius eye; *h*, heart, beneath it the ovary and digestive tract; *sp*, spermatophores; *1*, *2*, first and second antennæ; *3*, mandibles; *4*, maxillæ; *5*, maxilliped; *6–10*, swimming feet.

head (6), thorax (5), and abdomen (5)—of the animal. (In *Cyclops* the first thoracic segment is fused with the head, the first two abdominal segments are fused—fig. 7.) The terminal abdominal segment is two-forked, forming the 'furca.' While the abdomen lacks appendages, the thorax bears typical biramous appendages, consisting of a two-jointed basiopodite, the basal joint being frequently united with its fellow of the pair for common motion (fig. 410, *I*). Exopodite and endopodite, usually three-jointed, are fringed with bristles. Usually the fifth pair of thoracic appendages are not so well developed, and in some cases are represented by two bunches of bristles.

The two pairs of antennæ are frequently similar in size (whence the old name *Cyclops quadricornis*). The first pair are always uniserial and in the males may be hooked near the base for clasping; the second are sometimes biramous (fig. 410, *II*). The mandible (fig. 410, *III*, *V*) is instructive, since a study of several species shows that it is derived from a schizopodal condition and that the first basal joint alone is used for chewing, the rest being reduced to a palpus of varying development. Both basal joints of the maxillæ (fig. 410, *IV*) can be used in eating. Two maxillipeds (formerly regarded as the separated branches of an appendage) mark the termination of the head (fig. 422, *5*); both are hooked for holding the food.

The internal anatomy is simple. There is no liver, and the straight intestine (fig. 422) runs without marked changes in size to the anus between the branches of the furca. The visual organ is the unpaired nauplius eye (which has given the name to one genus, *Cyclops*). It lies directly on the brain. The ventral chain has its ganglia irregularly distributed. Gills are always absent, as are usually the heart and blood-vessels. Only in a few parasitic forms are there tubes which have been interpreted as parts of a vascular system; in some free forms there is a short saccular slowly pulsating heart. The gonads are unpaired in both sexes, but the sexual ducts, which open at the base of the abdomen, are paired. The females possess a receptaculum seminis distinct from the oviducts, to which the male attaches the spermatophores packed with sperm (fig. 422, *sp*). As the eggs leave the oviduct they are fertilized by the sperm issuing from the spermatophores, and numbers are enclosed in a gelatinous substance, thus producing bundles of eggs, the so-called egg-sacs, attached to the abdomen, by which one can easily recognize the females (fig. 7). A nauplius hatches from the egg, and by budding segments and appendages at the hinder end, and by a change of the nauplius appendages into antennæ and mandibles, passes through a 'cyclops-stage' into the adult.

The Copepoda have clearly descended from some phyllopod-like form. The poorly developed ventral chain, the loss, partial or complete, of a circulatory system, and the absence of gills are all evidences against the view which would consider them primitive.

Order I. Eucopepoda.

The forms to which the foregoing description will apply are the Eucopepoda, and include many species, which often occur in enormous numbers in both fresh and salt water, forming the larger proportion of the plankton. They thus furnish the most important food supply not only for fishes but for those giants among mammals, the baleen whales. *Cetochilus septentrionalis* occurs at times in such myriads that the sea for long distances is colored red.

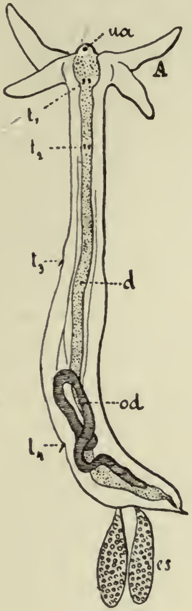


FIG. 423.

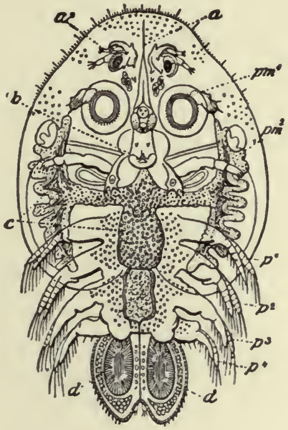


FIG. 424.

FIG. 423.—Female *Lernœocera esocina.* (From Lang, after Claus.) *A*, armlike processes of anterior end; *d*, digestive tract; *es*, egg-sacs; *od*, oviduct; t_1–t_4, rudimentary thoracic appendages.

FIG. 424.—*Argulus foliaceus.* (From Ludwig-Leunis.) *a*, sting; *a'*, antenna; *b*, mouth; *c*, intestine with liver; *d*, abdomen; pm^1, pm^2, first and second maxillipeds; p^1-p^4, biramous feet of thorax.

The CYCLOPIDÆ, with no heart and paired egg sacs, are fresh-water forms; *Cyclops* * (fig. 7). CALANIDÆ, fresh water and marine; heart present, single egg-sac. *Diaptomus*,* fresh water (fig. 422); *Cetochilus*,* *Pontilla*,* marine. HARPACTIDÆ, creeping forms, mostly marine; *Canthocamptus*,* fresh water. The CORYCÆIDÆ, which are half parasitic and include the wonderfully iridescent *Sapphirina* * (upon pelagic animals, as

Salpa), and the NOTODELPHIDÆ, parasitic in the gills of ascidians, form a transition to the next order.

Order II. Siphonostomata (Parasita.)

There are also Copepoda to which the account in large type will not apply, animals of such strange appearance that many of them were long regarded as parasitic worms (figs. 6, 423, 425). Their mandibles are altered to piercing bristles and enclosed in a piercing proboscis formed of upper and lower lips. With this sucking organ they bore into the skin or gills of fishes. They have cylindrical forms or bodies of the most bizarre shapes, in which frequently no segmentation is visible, while the appendages are rudimentary or even entirely lost. Indeed one would not recognize them as arthropods save for the following features:

(1) Most of them have the typical Copepod egg-sacs (sometimes elongate and spirally coiled) attached to the hinder end. (2) In the course of years a complete series of intermediate forms has been found, allowing one to trace, step by step, the alterations of form from that of the free-living species to that of the most modified parasites. (3) Ontogeny is convincing. Most parasitic Copepoda leave the egg as a nauplius and pass through a Cyclops-stage before attaching themselves to fishes and becoming the highly degenerate parasites. These parasites are always females. The males scarcely pass the Cyclops-stage, copulate with the females and then die, or if they pass through the metamorphosis, they remain small and different in appearance. They occur attached to the female near the genital openings. There is thus here a marked sexual dimorphism.

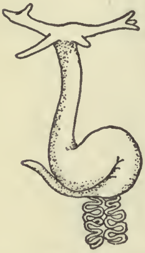


FIG. 425.—*Lernæa branchialis**(orig.)

The ARGULIDÆ (sometimes, but without warrant, made a distinct sub order, Branchiura) are fresh-water forms with compound eyes, liver lobes, and the second maxillipeds metamorphosed into suckers. *Argulus* * (fig. 424) causes considerable mortality to fish. The marine and brackish-water CALIGIDÆ (*Caligus* *) have similar habits. LERNÆOPODIDÆ. Fish parasites with maxillæ united into an adhesive organ. *Achtheres* * (fig. 6), parasitic on perch. LERNÆIDÆ; worm-like parasites. *Lernæa branchialis*,* common on gills of cod; *Lernæocera* * (fig. 423), on pike; *Penella.**

Sub Class IV. Ostracoda.

Like the Cladocera and the Estheriidæ the Ostracoda are enclosed in a bivalve shell, which, when closed, includes not only the body but the head and appendages as well, these being protruded when the shell is opened. The valves are closed by an adductor muscle, opened by a hinge ligament like that of lamellibranchs. This resemblance to the molluscs is heightened by lines of growth upon the shell.

The antennæ, the first simple, the second frequently two-branched, are used for swimming and creeping, and are bent backwards and provided with numerous joints and hairs. The following appendages (mandible, maxillæ, and three pairs of legs) vary greatly from genus to genus. The internal structure is also variable. The Ostracoda are largely bottom forms and live in fresh and brackish water as well as in the sea.

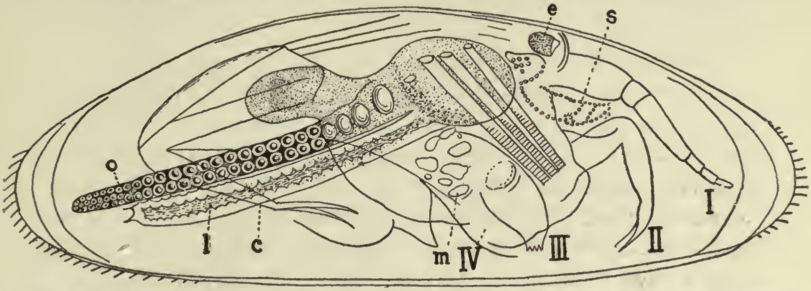


Fig. 426.—*Cypris fasciatus*, adult female. (After Claus.) *I–IV*, appendages; *c*, furca; *e*, eye; *l*, liver; *m*, adductor muscle of shell; *o*, ovary; *s*, shell gland.

Cypridinidæ. First two pairs of legs maxillary in character, the last developed into a hook for cleansing the shell; heart present; marine. *Cypridina*.* Cyprididæ. First pair of legs maxillary in character; heart lacking; fresh water. *Cypris*,* *Candona*.*

Sub Class V. Cirripedia.

The cirripeds, or barnacles, differ from all other crustacea in that they have lost their locomotor powers and live attached to rocks, floating timber, and the like. In some cases they attach themselves to other animals, as crabs and molluscs, or, as in the case of *Coronula*, to whales. This leads in *Anelasma* and the Rhizocephala to a true parasitism, the barnacle not only attaching itself to an animal but sucking its juices as food.

The attachment is by the dorsal surface in the neighborhood of the head, and is initiated by the first antennæ, in which is a cement gland secreting a rapidly hardening cement. The region of fixation in the Balanidæ (fig. 427) lies in the plane of the head; in the Lepadidæ it is drawn out into a long muscular stalk (fig. 114). To this attached life are related all the peculiarities of structure.

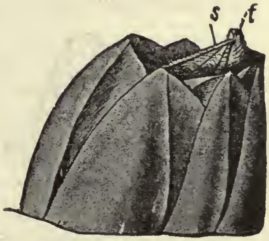


Fig. 427.—*Balanus hameri*,* acorn barnacle. (From Lang, after Darwin.) Formed of rostrum, lateralia, and carina, the operculum of scuta (*s*) and terga (*t*).

It is clear that a fixed animal has greater need of protection than one which can flee from its enemies, therefore we find not only a right and left mantle and a shell capable of complete closure, like that of an ostracode, but also in this calcified plates, the scuta and terga (figs. 114, 427, *s*, *t*), the first cephalic, the other posterior, in position.

Between the pairs of these is the gap through which the feet are protruded. Besides there are other calcified portions, one of which, the carina (fig. 114, *c*), corresponds to the hinge-line of the ostracode and in some Lepads is supplemented by a farther unpaired piece, the rostrum. In the Balanidæ the rostrum and carina are much stronger, while between them other paired pieces, the lateralia, are intercalated. Lateralia, rostrum, and carina arise from a base (usually calcareous) and form a capsule, closed above by a double valve formed of the paired scuta and terga, between which, when open, the animal can be seen (fig. 427).

The body in both lepads and balanids has essentially the same structure. It is flexed ventrally, so that mouth and vent are near each other, and bears six pairs of feathered feet, or cirri, which, when extended, become widely separated and form a most efficient means of straining small organisms from the water and conveying them to the mouth. These feet are biramous, with their branches ringed and thickly haired. Behind them is a rudimentary abdomen and an elongate penis; while the mouth is surrounded by a pair of mandibles and two pairs of maxillæ.

In internal structure the most noticeable feature is that the animals, in contrast to almost all other arthropods, are hermaphroditic, a condition possibly correlated with their sedentary life and the consequent need of self-impregnation. Yet it is to be remembered that the common forms have a long penis, so that these animals, crowded closely together, can fertilize each other. In cases of several species which live solitary complementary males occur. These are very small, purely male forms, with extremely simple structure (fig. 428), which live inside the mantle cavity near the genital openings. The unsegmented body is enclosed in a sac (a soft-skinned shell), and anchored by the antennæ. The long penis protrudes from the mantle. In the genus *Scalpellum* there are purely hermaph-

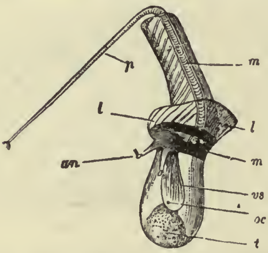


FIG. 428.—Male of *Alcippe lampas*. *an*, antenna; *l*, mantle lobes; *m*, muscles; *oc*, ocellus; *p*, penis; *t*, testis; *vs*, seminal vesicle.

roditic species, hermaphroditic species with complemental males, and purely diœcious species.

Since the hard shells of the barnacles resemble those of the molluscs, it is not to be wondered that these forms were long regarded as belonging to that group. It was not until the development (fig. 429) was studied that the error was corrected. A large nauplius comes from the egg and later is metamorphosed into a second larval stage with bivalve shell which, from its appearance, is called the cypris-stage. This becomes fixed and develops into the adult, losing the compound eyes and retaining the nauplius eye.

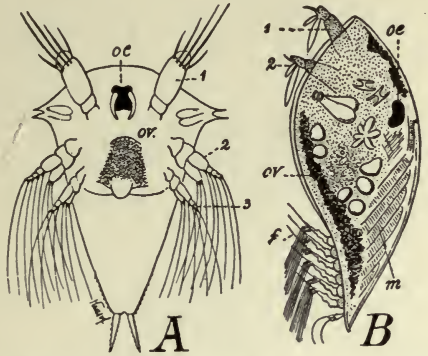


FIG. 429.—Nauplius (*A*) and Cypris (*B*) stages of *Sacculina carcini.* (After Delage.) *1*, *2*, antennæ; *3*, mandible; *f*, cirrhous foot; *m*, muscles; *oc*, nauplius eye; *ov*, anlage of ovary.

Order I. Lepadidæ.

Stalked cirripeds, with shell largely formed of scuta, terga, and carina; other parts may be added. *Lepas anatifera** (fig. 114) is the goose barnacle, which owes its common name to a mediæval myth which claimed that the Irish (or bernicle) goose developed from these animals. *L. fascicularis*,*(fig. 430), abundant floating on the eastern coast. *Anelasma squalicola*, a thin-skinned barnacle, is parasitic on sharks and forms a transition to the Rhizocephala.

Order II. Balanidæ.

Sessile cirripeds with calcareous shell formed of carina, rostrum, and lateralia; scuta and terga forming the valves (fig. 427). *Balanus balanoides*,* common on our coast. *Coronula diademata*, attached to the skin of whales.

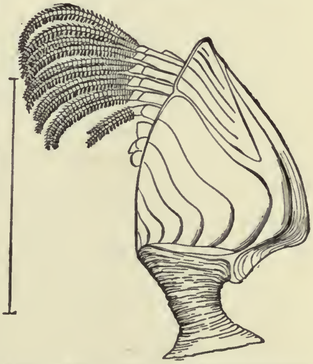


FIG. 430. — *Lepas fascicularis*,* goose barnacle. (From Smith.)

Order III. Rhizocephala.

These forms differ so much from the other cirripeds as to demand separate mention. They are parasitic on the abdomens of various decapod crabs and consist of a stalk which penetrates the body of the host and a body which remains outside. The stalk, which branches in a root-like manner, penetrates the cephalothorax and absorbs its juices. Since the stalk furnishes the food, an alimentary canal is absent. The body lacks all appendages, is enclosed by a soft-skinned mantle, and is almost entirely filled with the gonads. Since these forms lack, as adults, all arthropodan features, their position is only settled by their development, which shows (fig. 429) no great difference from that of other cirripeds. These forms are rare on the American coast. *Sacculina*, *Peltogaster*.*

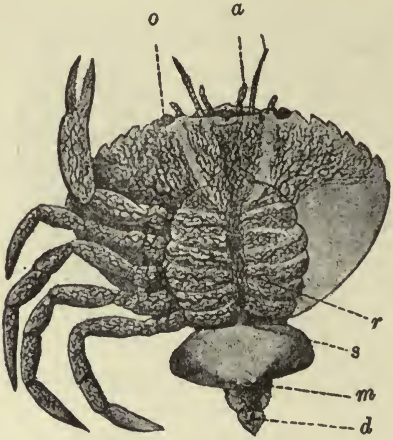


FIG. 431.—*Sacculina carcini* attached to *Carcinus mœnas*, whose abdomen is extended. *m*, shell opening; *r*, network of roots ramifying the crab; *s*, stalk; *a*, *o*, *d*, antennula, eye and anus of the crab.

Two more orders, ABDOMINALIA and APODA, parasitic in the mantle and shells of molluscs and other cirripeds, scarcely need mention.

Sub Class V. Malacostraca.

The Malacostraca are sharply marked off from the other Crustacea by having a body which consists of twenty segments, of which seven are abdominal (*Nebalia* has twenty-one, eight abdominal). The excretory organs are represented by the antennal glands, and shell glands are lacking except in some Isopoda. The male genital ducts open on the thirteenth, the female on the eleventh, segment.

Legion I. Leptostraca.

The Leptostraca connect the Phyllopoda with the higher groups. They have twenty-one somites, eight abdominal, eight thoracic, and five cephalic, and this and the openings of the genital ducts ally them to the Malacostraca. On the other hand the bivalve carapace covering the cephalothorax and part of the abdomen, and the leaf-like thoracic feet, are phyllopodan. They have an antennal gland and a rudimentary shell gland; an elongate heart which extends through cephalothorax and abdomen; and compound stalked eyes. The few species are all marine and belong to the genus *Nebalia*. *N. bipes* * (fig. 432).

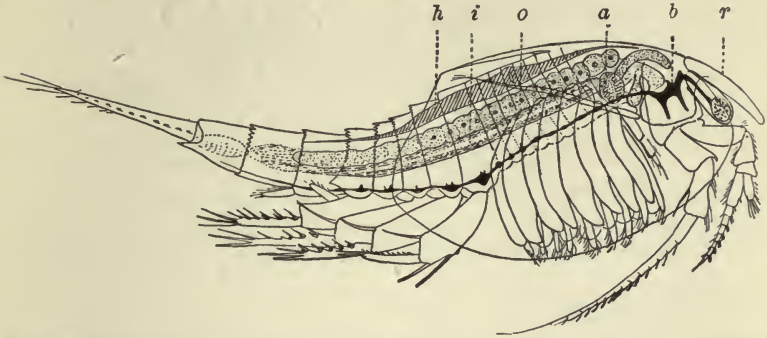


Fig. 432.—*Nebalia bipes.** (After Sars.) *h*, heart; *i*, intestine; *o*, ovary; *a*, adductor of carapace; *b*, brain; *r*, rostrum.

Legion II. Thoracostraca (Podophthalmia).

The names given this division have reference, first, to the fact that the head and more or fewer of the thoracic segments are united into an immovable part, covered by a firm carapace; second, that the compound eyes (except in Cumacea) are placed at the ends of movable eye stalks, a condition which has possibly arisen from the inflexibility of the anterior part of the body. The first five appendages are always two pairs of antennæ, a pair of mandibles, and two pairs of maxillæ. The remaining pairs vary greatly in character and from one to three may be modified into maxillipeds, while the abdominal somites except the last (*telson*) usually bear appendages, at least in the female. There is usually a metamorphosis in development in which a nauplius-stage may appear, most frequently in the lower forms (schizopods), but even in the decapods (*Peneus*).

Order I. Schizopoda.

These are small forms, mostly marine, in which the cephalothorax is covered by a carapace with which some or all of the thoracic somites are firmly united. The eight thoracic feet retain throughout life a biramous condition and are used in swimming. The posterior pair of abdominal feet together with the telson form a caudal 'fin' by means of which the animal can swim backwards. The delicate skin permits of diffuse respiration, and gills are frequently lacking. In some genera plates from the legs of the female enclose a brood case beneath the cephalothorax, thus giving these forms the common name of opossum shrimps.

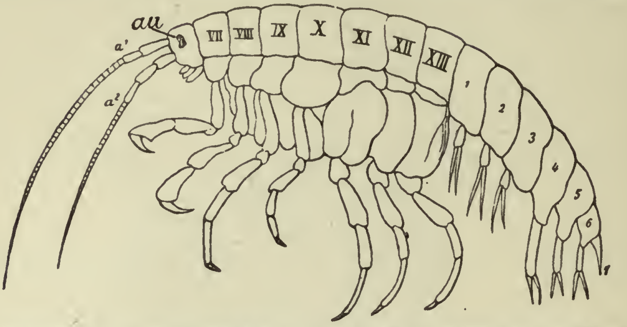


FIG. 433.—*Amphithoë.* (From Gerstäcker.) a^1, a^2, first and second antennæ; *au*, eye; *VII-XIII*, the seven free thoracic segments; *1-7*, abdominal segments.

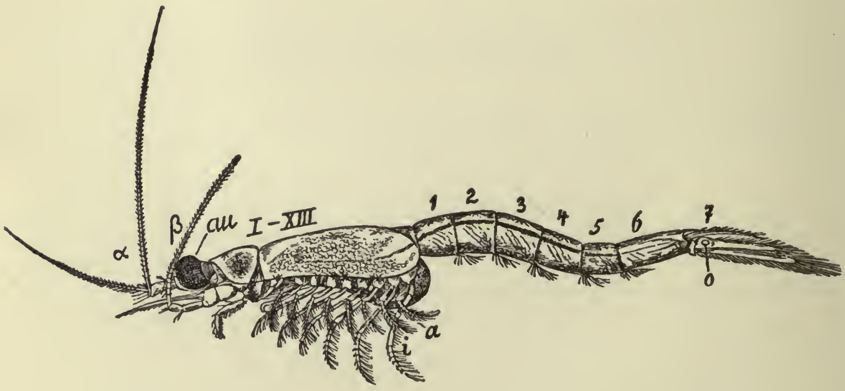


FIG. 434.—*Mysis elongata.* (From Gerstäcker.) α, β, first and second antennæ; *a*, exopodite; *au*, eye; *i*, endopodite; *o*, otocyst; *1-7*, abdominal somites.

The Mysididæ are the most widely distributed, several species of *Mysis* (fig. 434) occurring on our coasts and one in the Great Lakes. In these the endopodite of the sixth abdominal appendage contains an otocyst, with a calcic fluoride otolith. Other families are the Euphausiidæ and Lophogastridæ of the deeper seas.

Order II. Stomatopoda.

In structure of the cephalothorax these forms, known as mantis shrimps (from a resemblance to the insect, the praying mantis), have not advanced as far as the schizopods, since the last three thoracic somites remain free and are not covered by the carapace.

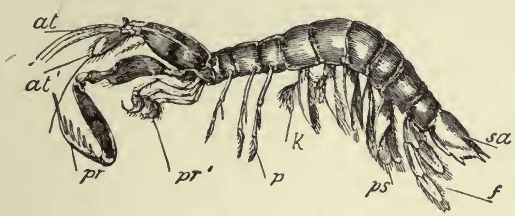


Fig. 435.—*Squilla mantis.* *at*, *at'*, first and second antennæ; *f*, sixth abdominal feet; *k*, gills; *p*, schizopodal thoracic feet; *pr*, *pr'*, raptorial feet; *ps*, pleopoda; *sa*, telson.

The appendages, however, are more differentiated, since only the three posterior thoracic feet are biramous and natatory. The four in front of these are prehensile and bear a pincer formed of the last two joints, the last being slender and usually toothed and closing in a groove of the penult joint like a knife blade in the handle. The first of these raptorial feet are the largest and are used in capturing fishes, etc. Since the thoracic feet are of little service for locomotion, the abdomen is long and stout, especially the caudal fin. The five anterior abdominal feet bear the gills, and correspondingly the elongate heart with many ostia extends into the abdomen. The transparent pelagic larvæ were formerly regarded as adults and described as *Alima* and *Erichthus*. *Squilla empusa* lives on our east coast, *Gonodactylus* in Florida. They are burrowing animals and deposit their eggs in their holes.

Order III. Decapoda.

The Decapoda is the most important group of Crustacea, since it contains the shrimps, lobsters, crayfish, and crabs. It agrees with the Schizopoda in having a cephalothorax composed of thirteen fused somites, but differs in the structure and function of the thoracic extremities. Only the last five pairs (whence the name Decapoda) are locomotor. These lose the exopodite during development and become strong walking legs, terminated either with claws or pincers (chelæ). Usually the first pair is distinguished from the others by its size and by being chelate, and becomes not locomotor but grasping in function. In the development of a chela the penult joint sends out a strong process, the 'thumb,' which extends as far as the last joint (the 'finger'), which closes against it.

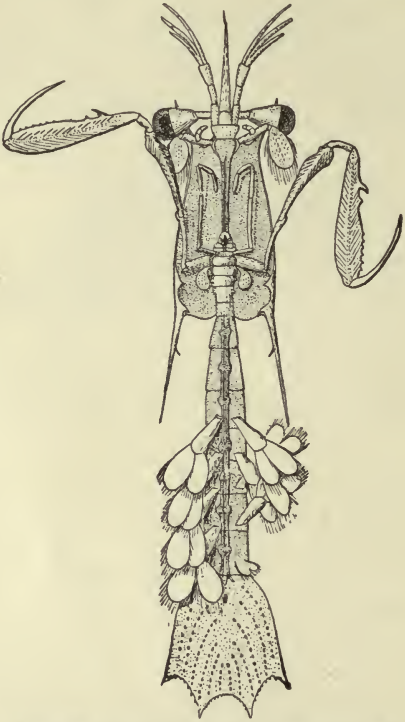


Fig. 436.—Erichthus stage of *Squilla* (orig.).

The mouth parts—a pair of mandibles, two pairs of maxillæ, and three pairs of maxillipeds (fig. 404)—lie in front of the first pair of legs. The maxillipeds (7, 6, 5)show clearly a biramous condition, while the maxillæ (4, 3) retain considerable of the original phyllopod character. In the mandibles (2) there is always a strong basal joint, the edge of which serves as a jaw, while this may bear additional joints, the *palpus*. Behind the mouth are a pair of scales, the *paragnaths* or *metastoma*, formerly regarded as appendages. The antennæ are usually distinguished from their size as antennæ (second pair) and *antennulæ* (first pair, fig. 404). They have large basal portions, which in the antennulæ bear two many-jointed flagella, while the antennæ proper have but a single though usually much larger flagellum. On the basal joint of the antennulæ is the auditory organ (p. 412), while the green gland opens on the basal joint of the antennæ (fig. 439, *gd*).

When the abdomen is not rudimentary (as in the crabs) the appendages of the sixth abdominal segment together with the telson form a strong caudal fin (fig. 439); the other appendages (fig. 404, *I*) are small, biramous organs to which, in the female, the eggs are attached. In the female the first pair is reduced, but in the male except in Palinuridæ this pair is well developed, curiously modified, and serves as a copulatory (intromittent) organ. The condition of these appendages as well as the openings of the genital ducts—on the base of the third walking foot in the female, the fifth in the male—serve at once to distinguish the sexes. Frequently also the males have the larger pincers.

The thickness of the integument prevents diffuse respiration and accounts for the numerous gills (fig. 437) which are attached to the bases of the appendages (maxillipeds and walking feet) or to the sides of the body near them. (In the Thalassinidæ—forms near the Astacidæ—the gills are on the abdominal appendages). These gills are not visible externally, for the carapace extends down on the sides of the body as a fold (*branchiostegite*) over them, thus enclosing them in a branchial chamber. A process of the second maxillæ—the *scaphognathite*—plays in this branchial chamber and pumps the water over the gills, the water flowing out near the mouth. All decapods can live some time out of water, a fact readily explained when we remember that they retain some water in the gill chamber, which keeps the gills in a moist condition. In some of the tropical land crabs which live almost exclusively on land there is a true aerial respiration, the lining of the gill chamber becoming modified into a kind of lung traversed

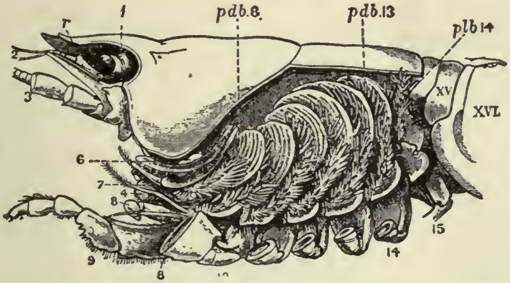


FIG 437.—Gills of *Astacus* exposed by cutting away the branchiostegite. *pdb*, *plb*, podo- and pleurobranchia of the corresponding segments; *r*, rostrum; *1*, stalked eyes; *2*, *3*, antennæ; *4-6*, mandibles and maxillæ; *7-9*, maxillipeds; *10*, *14*, bases of thoracic feet; *15*, first pleopod.

by numerous blood-vessels. In *Birgus latro* the gill chamber is divided into two portions (fig. 438), the upper part being pulmonary, the lower containing the reduced gills.

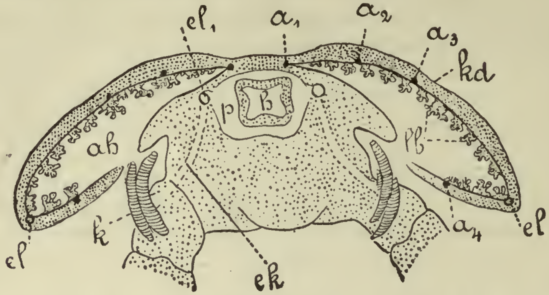

el₁
a₁
a₂
a₃
kd
p
h
ah
pb
k
ek
el
a₄
el

FIG. 438.—Diagrammatic section through *Birgus latro*, showing lungs. (From Lang, after Semper.) a_1, a_4, afferent blood-vessels; *ah*, pulmonary chamber; *ek*, *el*, *el′*, efferent blood-vessels; *h*, heart; *k*, gills; *kd*, branchiostegite; *p*, pericardium.

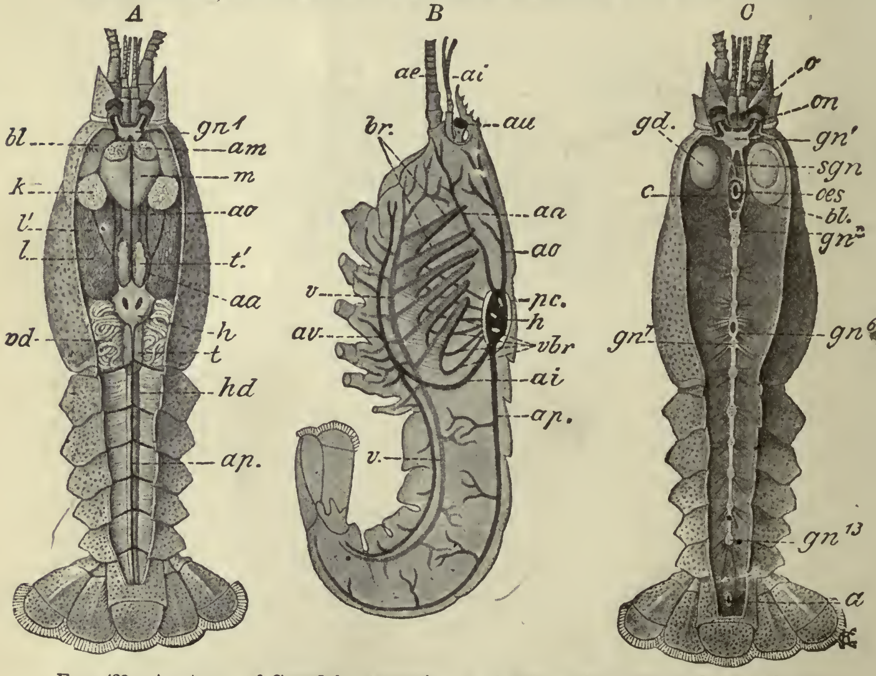

A
B
C
bl
k
l′
l
vd
gn¹
am
m
ao
t′
aa
h
t
hd
ap.
ae
ai
au
br.
aa
ao
v
av
pc.
h
vbr
ai
ap.
v.
o
on
gd.
gn′
sgn
c
oes
bl.
gn²
gn⁷
gn⁶
gn¹³
a

FIG. 439.—Anatomy of Crayfish (*Astacus*). *A*, dorsal surface removed; *B*, scheme of circulation; *C*, viscera removed, showing green gland and nervous system. *a*, anus; *aa*, hepatic artery; *ae*, antenna; *ai*, antennula, also sternal artery; *am*, muscles of stomach; *ao*, ophthalmic artery; *ap*, abdominal artery; *av*, ventral artery; *bl*, urinary bladder; *br*, gill arteries; *c*, œsophageal commissures; *gd*, green gland; *gn′*, brain; gn^{2-13}, ganglia of ventral chain; *h*, heart; *hd*, intestine; *k*, mandibular muscles; *l*, *l′*, liver and its duct; *m*, stomach; *o*, otocyst; *oes*, œsophagus; *on*, optic nerve; *pc*, pericardium; *sgn*, sympathetic nerve; *t*, *t′*, unpaired and paired portions of testes; *v*, ventral blood sinus; *vd*, vas deferens; *vdr*, veins from gills to heart.

Correlated to this localized respiration is the nearly closed circulatory system (figs. 439, *A*, *B*). The heart (*h*), a compact pentagonal organ, receives its blood from the pericardial sinus (*pc*) through three pairs of ostia, and forces it out through five arteries to the capillary regions of the body. The venous blood collects in a large venous sinus at the base of the gills (*v*), passes thence through gills, and is returned by several branchial veins (*vbr*) to the pericardium.

The alimentary canal is straight and has only one conspicuous enlargement, the so-called stomach (fig. 439, *A*, *m*), divided into two portions, an anterior sac (cardiac pouch), lined with chitinous folds and teeth and serving to chew the food and bearing in its walls the so-called 'crab-stones,' which are masses of calcic carbonate stored up to harden the armor rapidly after the molt. The second or pyloric portion of the stomach is guarded by hairs and serves as a strainer, allowing only food sufficiently comminuted to pass. The two liver lobes—voluminous masses of branched glandular tubes (*l*) open just behind the stomach.

The two antennal glands (fig. 439, *C*, *gd*), each provided with a large urinary bladder (*bl*), are dirty green in color, whence the name green glands often applied to them. The gonads (figs. 440) lie close beneath the heart, those of the two sides

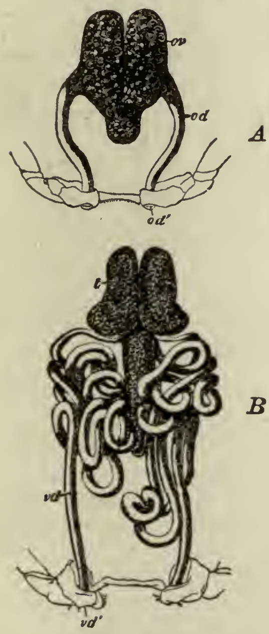


Fig. 440.

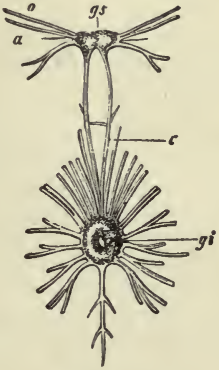


Fig. 441.

Fig. 440.—Reproductive organs of (*A*) female and (*B*) male crayfish. (From Huxley.) *od*, oviduct; *od'*, its opening on 11th appendage; *ov*, ovary; *t*, testes; *vd*, vas deferens; *vd'*, its opening on 13th appendage.

Fig. 441.—Nervous system of crab, *Carcinus*. (From Gegenbaur.) *a*, antennal nerves; *c*, œsophageal commissures; *gi*, fused ventral chain perforated for sternal artery; *gs*, brain; *o*, optic nerve.

being united behind, while their ducts remain separate. The structure of the nervous system is in part dependent upon that of the abdomen. In the Macrura (fig. 439, *C*) the ventral chain consists of six ganglia in the thorax, six in the abdomen, but in the Brachyura (fig. 441) these all flow together in a common mass, connected with the brain by two long œsophageal commissures.

The development of most decapods is interesting from the number of larval forms. As a rule a zoea (fig. 415) is hatched from the egg; this passes next into a Mysis-stage (fig. 442) in which head, thorax, and abdomen are distinct, the thorax bearing biramous feet like those of schizopods—a proof of the origin of the simple feet from the biramous type. In the crabs (Brachyura) the Mysis-stage is replaced by a Megalops (fig. 443), in which the abdomen is well developed but the feet have lost their biramous character. In some prawns (*Peneus*) the series is rendered more complete by the appearance of a nauplius and a metanauplius with many appendages, before the zoeal stage. In the crayfish and many land crabs the metamorphosis has been lost, but the lobster leaves the egg in the Mysis-stage. Differences may occur even in the same species; thus in the European *Palæmonetes varians* the embryo, in the sea, leaves the egg as a zoea; in fresh water in the Mysis-stage.

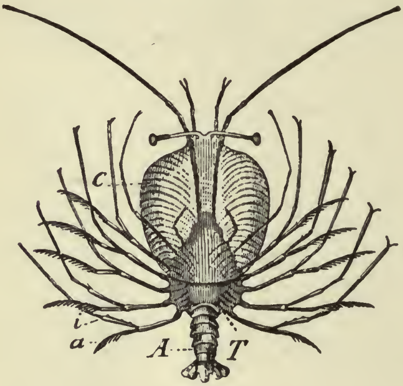


FIG. 442.

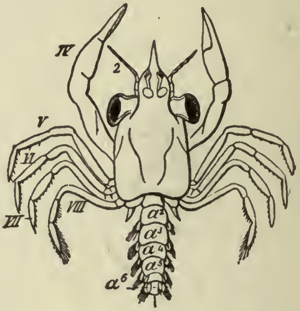


FIG. 443.

FIG. 442.—Phyllosoma larva (Mysis-stage) of *Palinurus*. (After Gerstäcker.) *A*, abdomen; *C*, head; *T*, thorax; *a* and *i*, exopodites and endopodites of thoracic feet.
FIG. 443.—Megalops larva of *Portunus*. (From Lang, after Claus.) *2*, antennæ; *IV–VIII*, thoracic appendages; a^2–a^6, abdominal somites (a^6 is the seventh).

Sub Order I. MACRURA. Abdomen well developed; antennæ long; ventral nerve chain elongate; no megalops-stage in development. CARIDEA. Body compressed; no sutures on carapace; feet weak, external maxillipeds pediform; a large scale on the second antennæ. In the PENEIDÆ there are weak exopodites. *Peneus*,* *Sicyonia*.* PALÆMONIDÆ, mandibles bifid at tip. *Palæmon*, *Alpheus*,* *Hippolyte*,* *Pandalus*.* In the CRANGONIDÆ the mandible is simple. *Crangon*,* *Sabinea*.*

Astacoidea. Carapace crossed by a transverse groove. The **Astacidæ** have well-developed chelæ. *Cambarus* * includes the crayfish of the eastern states; those of the Pacific coast and Europe belong to *Astacus.** The lobsters belong to *Homarus.** **Palinuridæ** (Loricata), no chelæ,

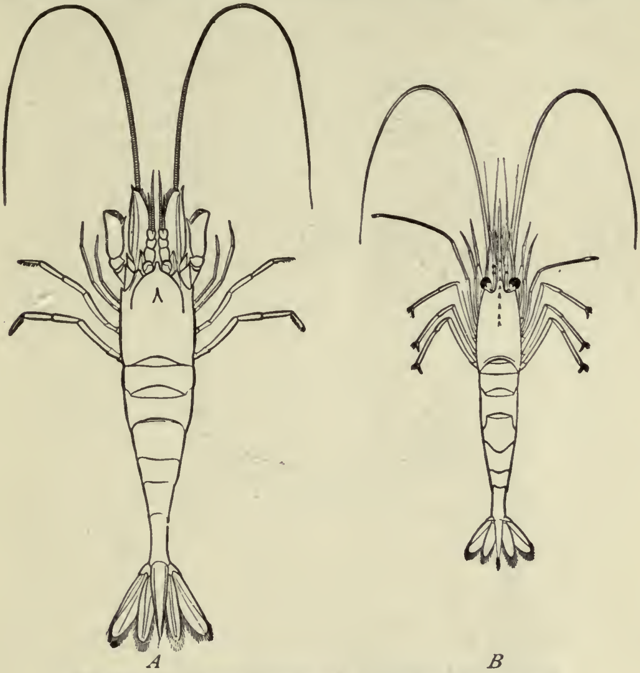


Fig. 444.—*A*, *Crangon vulgaris* *; *B*, *Pandulus montagui.**

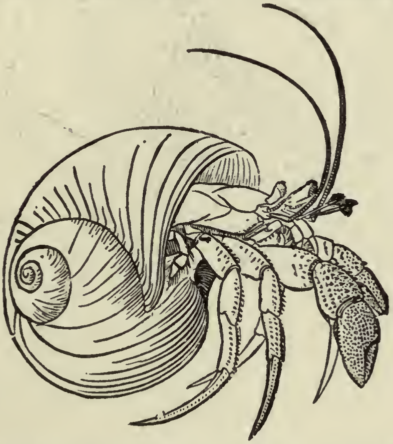


Fig. 445.—*Eupagurus bernhardus*, hermit crab. (From Emerton.)

body with heavy armor; larva leaf-like and transparent 'glass crabs,' called Phyllosomæ (fig. 442). *Palinurus,** spiny lobster. PAGURIDEA, hermit crabs; abdomen reduced, soft-skinned, and hidden for protection in a snail shell which the animal carries about, which habit has resulted in a spiral twisting of the abdomen. Some hermits (*Eupagurus*) carry sea anemones or hydroids on their shell, cases of symbiosis (p. 170). *Eupagurus,* Clibanarius.** Allied is *Birgus*, the palm crab of the East

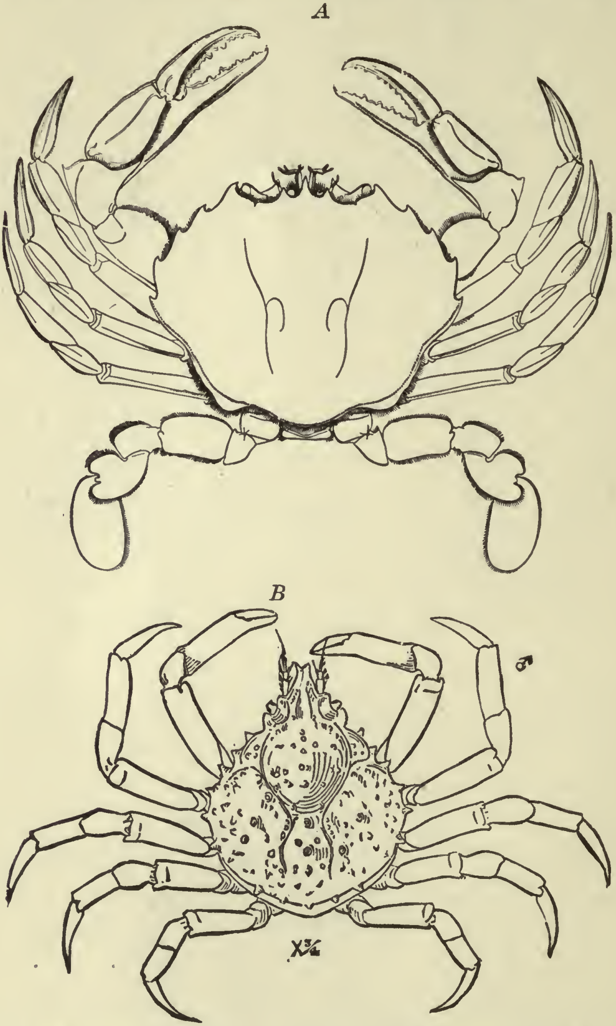


Fig. 446.—*A*, *Platyonichus ocellatus,** lady crab; *B*, *Libinia emarginata,** spider crab (From Emerton.)

Indies, which is said to climb palm trees for the cocoanuts, which it eats. Its respiratory organs have been referred to on p. 432.

Sub Order II. BRACHYURA. Body depressed; abdomen rudimentary and folded in a groove under the cephalothorax; antennæ short; never more than one pair of feet chelate; ventral nerve cord concentrated (fig. 441). Omitting some inconspicuous groups like the porcellain crabs (PORCELLANIDÆ), the HIPPIDÆ, and the LITHODIDÆ, which are united as a group of Schizosomi from the fact that the last thoracic segment is free from the carapace and its appendages are rudimentary, the sub order is usually divided as follows: LEUCOSOIDEA (Oxystomata). Body oval or triangular, area of mouth parts triangular, the apex anterior. *Calappa*, *Matuta*,* *Hepatus* * of warmer seas. OXYRHYNCHA (Maioidea). Cephalothorax triangular, narrowed in front; mouth area (as in the following tribes) quadrilateral. Mostly tropical. *Hyas*,* *Libinia*,* *Pugettia*,* spider crabs. CYCLOMETOPA. Body broader than long, regularly arcuate in front. CANCRIDÆ, with last pair of feet pointed. *Cancer*,* shore crab; *Panopeus*,* mud crab. PORTUNIDÆ, with last pair of feet flattened paddles. *Platyonichus* *; *Neptunus hastatus*,* when thin-skinned after molting, is the 'soft-shell crab' of the markets. CATOMETOPA. Front of carapace nearly straight; body from above nearly quadrilateral; *Gelasimus*,* the fiddler crabs of our warm shores; *Pinnotheres ostreum*,* common in oysters; GECARCINIDÆ (*Uca*, etc.), land crabs of the tropics, which only go to the sea at the reproductive season to lay their eggs.

Order IV. Cumacea.

Small marine forms with sessile eyes, three or four free thoracic somites; appendages biramous; a brood sac beneath the cephalothorax. Of interest because combining arthrostracan and thoracostracan features. *Diastylis* (fig. 447).

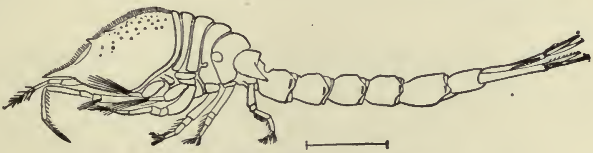


FIG. 447.—*Diastylis quadrispinosus.*

Especial interest also centres in the little known *Anaspides tasmaniæ* from lakes in Tasmania, which unites schizopod and amphipod characters. It has the stalked eyes, caudal fin, and biramous feet of a schizopod; otocysts in the antennulæ like a decapod; but agrees with the amphipods in shape of body and in free thoracic segments. The epipodial plates are paralleled elsewhere only in carboniferous species, with which these forms apparently are closely allied.

Legion III. Arthrostraca (*Edriophthalmata*).

Although the head of the Arthrostracan consists of six segments, it is remarkably short. It bears six pairs of appendages, one of the normal thoracic pair being added to it as maxillipeds. Eyes, when present, are aggregates of ocelli situated on the sides of the head. There are seven thoracic segments, the appendages of which are walking feet which lack exopodites. The abdominal appendages, when present, are always biramous, the telson never bearing appendages, and in the Amphipods is greatly reduced, sometimes being split nearly its whole length.

The nervous system (figs. 75, 448) is of the ladder type. The alimentary canal is straight and has an anterior enlargement, the chewing stomach, behind which empty one or more pairs of long liver tubes, while in a few Amphipods a pair of excretory tubes, the so-called Malpighian tubules, empty into the intestine near its end. Respiratory and circulatory systems vary so that they are best described in connexion with the two orders.

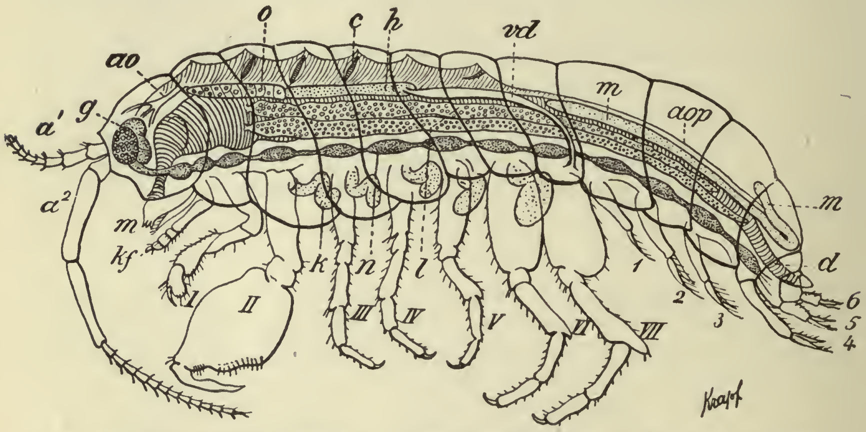


FIG. 448.—Male *Orchestia cavimana*. (After Nebeski.) a', a^2, antennæ; *ao*, *aop*, anterior and posterior aortæ; *c*, heart; *d*, digestive tract; *g*, brain and eye; *h*, testes; *k*, gills; *kf*, maxilliped; *l*, liver; *m*, excretory organ; *n*, ventral nerve cord; *o*, rudimentary ovary; *vd*, vas deferens; *I–VII*, thoracic feet; *1–3*, anterior, *4–6*, posterior abdominal feet.

Order I. Amphipoda.

The Amphipods are almost exclusively aquatic, a few species living on the shore near high-tide mark. A few live in fresh water (*Gammarus, Allorchestes*), the majority being marine. On land they move by a leaping motion, whence the common name, beach fleas. In swimming the abdomen is alternately bent against the breast and then forcibly straightened.

The body is usually strongly compressed from side to side. The thoracic feet generally bear large *epineural plates* (fig. 433), which extend the sides of the body downward, while on the inner side delicate gills or gill sacs (fig. 449, *br*) arise from their bases. In the female brood lamellæ (*brl*) are added—broad chitinous plates which enclose a brood chamber beneath the body in which eggs or young are carried. The three anterior pairs of abdominal feet are two-branched, richly haired, and serve to create currents of water which pass forward over the gills. The remaining abdominal feet, though biramous, are short and stout and form springing organs. The position of the gills explains why the abdominal part of the heart is degenerate and only the anterior thoracic portion with three pairs of ostia persists.

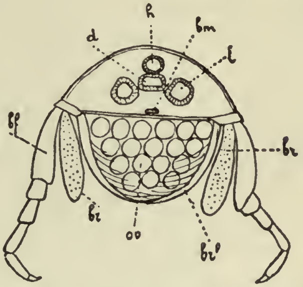


Fig. 449.—Cross-section of Amphipod (*Corophium*). (From Lang, after Delage.) *bf*, thoracic leg; *bm*, ventral nerve cord; *br*, branchiæ; *brl*, brood lamella; *d*, intestine; *h*, heart; *l*, liver: *ov*, eggs in brood chamber.

Sub Order I. HYPERINA. Large head and eyes; strong prehensile feet. Live attached to other pelagic animals on which they feed. *Hyperia medusarum* * lives on the jelly fish *Cyanea; Phronima*,* warmer seas.

Sub Order II. GAMMARINA. Head much smaller; abdomen well developed; are mostly free swimmers. Numerous species in the sea. *Gammarus* * occurs in shallow water, some being fluviatile; *Orchestia* * above tide marks. *Chelura terebrans* * destroys piles and other submerged wood.

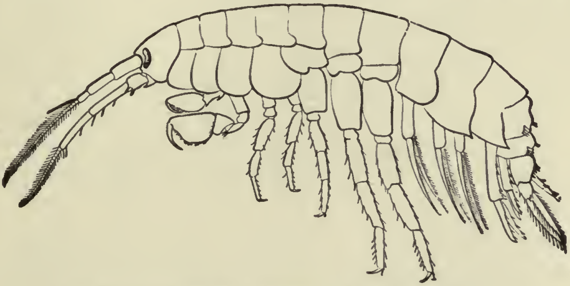


Fig. 450.—*Gammarus ornatus*.* (From Smith.)

Sub Order III. LÆMODIPODA. Parasitic or semi-parasitic forms in which the first (second) somite is fused to the head; appendages are lacking from some of the thoracic segments and the abdomen is reduced. Species of *Caprella* * are common on hydroids. *Cyamus ceti* is parasitic on whales.

Order II. Isopoda.

The Isopoda are readily distinguished from the Amphipoda by their depressed (*i.e.* horizontally flattened) bodies. The feet are adapted for creeping, and a brood pouch is formed as in the Amphipoda, but gills are lacking here since some of the abdominal feet are modified for respiration (fig. 451, *k*). In the abdomen, the somites of which exhibit a great tendency to fusion, the telson, as in all Malacostraca, is without appendages; the sixth somite bears, in the walking forms, long forked appendages (fig. 451); in the swimming species (fig. 452) they are flattened and, with the telson, make a swimming organ. The five anterior pairs of pleopoda are modified for respiration, by the expansion of the endopodites into thin-walled plates, while the exopodites and the whole first pair serve as opercula or gill covers. As a result of this position of the gills the heart (usually with two pairs of ostia) is abdominal in position.

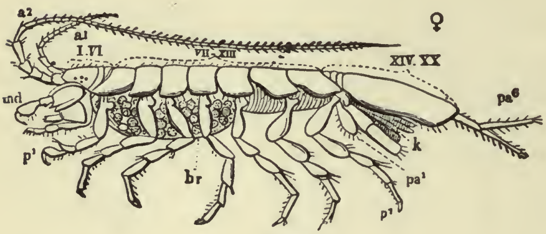


FIG. 451.

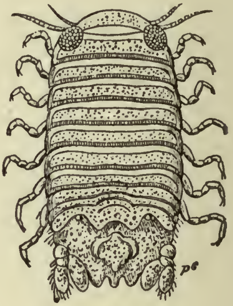


FIG. 452.

FIG. 451.—*Asellus aquaticus.* (From Ludwig-Leunis.) a^1, a^2, antennæ; *br*, brood pouch; *k*, pleopoda modified to gills; *md*, mandibles; p^1-p^7, thoracic feet; pa^1-pa^6, abdominal feet (pleopoda); *I-VI*, head; *VII-XIII*, thoracic segments; *XIV-XX*, abdominal segments, partly fused.

FIG. 452.—*Cymothoa emarginata.* (After Gerstäcker.) p^6, sixth pleopod.

In the terrestrial species the gills are adapted for breathing damp air. In *Porcellio* and *Armadillidum* the first or first and second opercula are permeated with a system of air tubes, which physiologically, though not morphologically, are comparable to the tracheæ of insects.

In the Isopoda the tendency to parasitism is greater than in the Amphipoda. Many swimming forms attach themselves to fishes and feed by boring with their mouth parts, which are modified for the purpose, into the skin. The Bopyridæ live in the branchial chamber of shrimps. *Cryptoniscus* is a shapeless sac which attaches itself to the stalk of *Sacculina* (p. 426), and, after causing the death of this parasite, uses its network of 'roots' for its own nourishment. The Entoniscidæ (fig. 453) attack

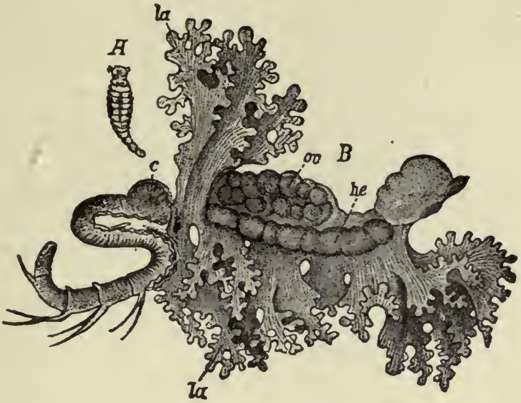


FIG. 453.—*Entoniscus porcellanæ.* (From Gerstäcker, after Müller.) *A*, male; *B*, female; *C*, heart; *he*, liver; *la*, brood lamellæ; *ov*, ovary.

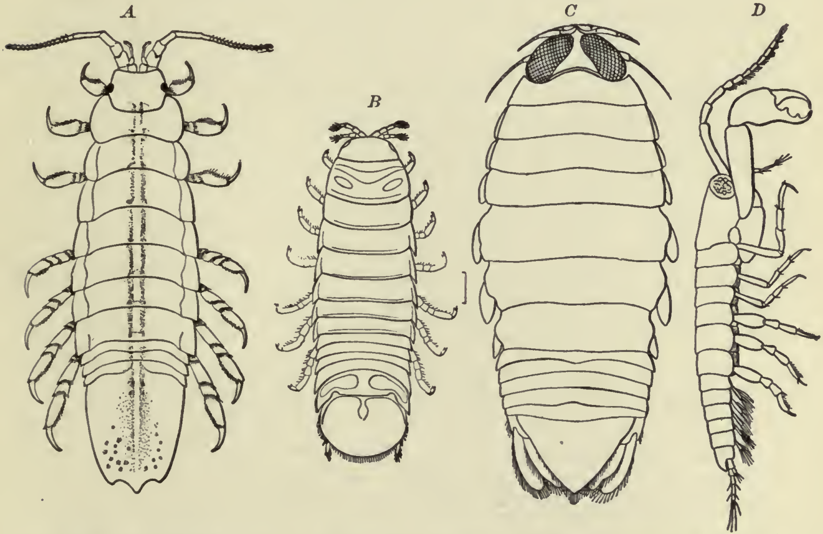


FIG. 454.—*A*, *Idotea irrorata* *; *B*, *Limnoria lignorum* *; *C*, *Ægа psora* * ('salve bug'); *D*, *Leptochela algiçola.** (After Harger.)

Decapoda and, pressing the skin before them, penetrate the interior. Their strange shape is largely due to the lobe-like brood lamellæ. They are usually hermaphroditic, but have besides complemental dwarf males (fig. 453, *A*).

Sub Order I. ANISOPODA. Six free thoracic segments; heart thoracic; first thoracic foot (on head) chelate; abdomen with swimming feet. A group intermediate between Amphipoda and other Isopoda. *Tanais*,* *Leptochela** (fig. 454).

Sub Order II. EUISOPODA. Seven free thoracic segments. ONISCIDÆ; terrestrial, familiarly known as sow bugs; *Ligia*, on seashore; *Porcellio*,* *Oniscus*,* *Armadillidum*,* 'pill bug.' ASELLIDÆ (fig. 451), fresh water. SPHÆROMIDÆ, head broad, body rounded and convex; *Sphæroma*.* *Limnoria lignorum** (fig. 454), the gribble, attacks submerged wood and is nearly as destructive as *Teredo*. IDOTEIDÆ, free-living, marine, with usually elongate bodies; *Idotea*,* *Cœcidotea*,* BOPYRIDÆ, parasitic on Caridea; body of female disc-like, asymmetrical, without eyes; *Bopyrus*.* CYMOTHOIDÆ, parasitic on fishes or in their mouths. *Cymothoa*,* *Æga*,* *Cirolana*.*

Sub Order III. ENTONISCIDA, parasites whose general features are described above. *Entoniscus*, *Cryptoniscus*.

Class II. Acerata.

The animals comprising this group were formerly divided among the tracheates (p. 408) and the Crustacea, but more recent studies show that, although differing widely in respiration, the forms included are closely allied in structure and development and present many differences from both Crustacea and from other tracheates (Insecta). The former views were based upon a confusion between analogy and homology, it being thought that tracheæ wherever found were homologous structures.

In the Acerata the body is usually divided into two regions, cephalothorax and abdomen, though in some cases (mites) the two regions become fused. The cephalothorax consists of six somites which always bear appendages, and these appendages are arranged in a circle around the mouth, the basal joints of one or more pairs frequently serving as jaws. None of these appendages are like antennæ (whence the name of the group). The abdomen consists of a varying number of somites, all of which may be free, or, again, may be fused into a common mass. These abdominal somites bear appendages in the embryo, but in the adults (except the Xiphosura) these are usually lost or so modified that their existence is only recognized by a study of development.

The alimentary canal is straight, without marked enlargements, and lacks a chewing stomach. The liver is large and opens into the intestine by two or more pairs of ducts. The nervous system has some or all of its ventral ganglia arranged in a ring around the œsophagus, and in many forms is enclosed in the ventral artery. Excretory organs, in the shape of nephridia, are frequently present and open to the exterior at the base of the second or the fifth pair of appendages. Malpighian tubes may occur, but these, unlike those of other tracheates, are entodermal in origin and hence not homologous with them.

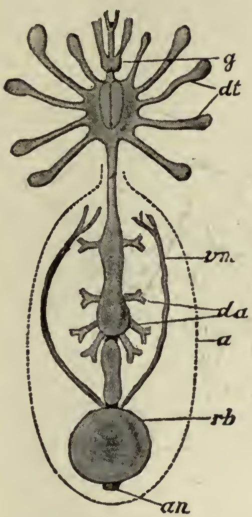


Fig. 455.

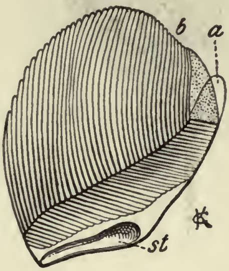


Fig. 456.

Fig. 455.—Digestive tract of *Ctenida cœmentaria.* (From Lang, after Dugès.) *a*, abdomen; *an*, anus; *da*, *dt*, diverticula ('liver') of midgut; *g*, brain; *vb*, rectal bladder (stercoral pocket); *vm*, excretory tubules.

Fig. 456.—Lung book of *Zilla cadophyla.* (After Bertkau.) *a*, a lung leaf separated from the other leaves, *b*; *st*, spiracle.

The respiratory organs are either gills, lungs, or tracheæ. The gills are borne on some of the abdominal appendages. The lungs are sacs on the anterior abdominal somites opening by narrow slits (fig. 461) to the exterior. The anterior wall of each lung sac is made up of thin plates arranged like the leaves of a book, and embryology shows that these lung books are gill books drawn into the ventral surface of the abdomen. The tracheæ in development pass through a gill-stage and a lung-stage, the tracheal tubes being outgrowths of the spaces between the lung leaves which penetrate all parts of the body.

The reproductive openings are on the basal somite of the abdomen. The spermatozoa are motile. The development is direct, there being no metamorphosis.

Sub Class I. Gigantostraca.

Marine forms with gills on the 2–6 abdominal appendages; bases of five pairs of cephalothoracic feet masticatory; a pair of median ocelli and a pair of compound eyes on the cephalothorax.

Order I. Xiphosura.

Cephalothorax large; abdomen terminated by a long spiniform telson. *Limulus polyphemus* of our east coast, commonly known as king crab

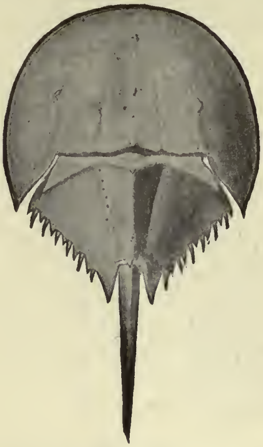


Fig. 457.

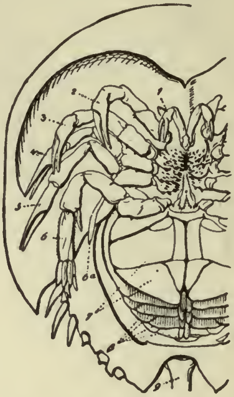


Fig. 458.

Fig. 457.—*Limulus polyphemus*,* horseshoe crab (orig.).

Fig. 458.—Ventral surface of *Limulus moluccanus*. (From Ludwig-Leunis.) *1*, cheliceræ; *2–5*, walking feet; *6*, pushing foot; *6*a, flabellum; *7*, genital operculum; *8*, gills (there should be five); *9*, base of telson.

or horseshoe crab. Other species on eastern shore of eastern continent. They burrow beneath the sand and mud of the bottom and feed on worms. In the spring they come to the shore to lay eggs.

Order II. Eurypterida.

Extinct Silurian and Devonian forms with small cephalothorax and large twelve-jointed abdomen. The animals are intermediate between the xiphosures and the scorpions. *Eurypterus; Pterygotus*. some species seven feet long.

Sub Class II. Arachnida.

Under this name are included a number of orders of greater or less extent which can be arranged around the spiders, or Aranea, as a centre. There is considerable modification of form, and the following account applies only to the more typical groups. In these the cephalothorax and abdomen are separated by a distinct line, and since the abdominal appendages almost entirely disappear in the adult, the number of somites can only be ascertained where their boundaries are evident. The number varies between six in the phalangids and thirteen in the scorpions.

The cephalothorax is, except in the Solpugidæ, a single piece which bears six pairs of appendages; the four posterior pairs, consisting typically of seven joints, are locomotor, so that the possession of eight legs is as characteristic for an arachnid as ten for a decapod or six for a hexapod. The first pair of appendages, the *chelicerœ* (fig. 459), are preoral, the second, or *pedipalpi*, beside that opening. The cheliceræ are short and consist of two or three joints, the terminal joint either folding back upon the other or, pincer-like, meeting an opposable thumb. In the spiders the last joint or claw is forced into the prey, introducing poison from a sac in the basal joint. The pedipalpi are elongate, leg-like, their basal joints often forming a lip, the other joints forming the palpus, which may end with a claw or a pincer.

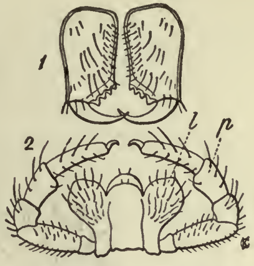


FIG. 459.—Mouth parts of *Epeira*. *1*, chelicera; *2*, pedipalpi; *p* palpus; *l*, basal plate.

The question has often been discussed as to whether the cheliceræ are the homologues of the antennæ of other arthropods. The embryological evidence, which cannot be detailed here, is in favor of their equivalence to the second antenna of the crustacea, and to the mandibles of insects.

Since the Arachnida usually suck their food, the œsophagus is frequently widened to a sucking stomach, behind which comes the true stomach, with which, as well as with the intestine, a number of so-called liver tubes may arise (fig. 455, *da, dt*). These may be restricted to the abdomen alone, as in the scorpions. The hinder part of the intestine is often enlarged into a rectal vesicle (stercoral pocket), just in front of which the excretory tubules (so-called Malpighian tubules) empty. These resemble the true Malpighian tubes of insects in function, but differ in being entodermal in origin. Besides there also occur coxal glands (modified nephridia), of which only one pair comes to development, and this may lose its external opening on the base of the appendage.

The œsophagus is always closely surrounded by a nerve ring composed of brain above and of part of the ventral chain on the sides and below, the thoracic and more or fewer of the abdominal ganglia entering into its composition (fig. 405, *D*). Of sense organs, besides tactile hairs, only the eyes (fig. 406), 2–12 in number, are well known. Hearing is well developed, but it is uncertain whether certain hairs on the legs and palpi are the seats of the recognition of sound. The function of the 'lyriform organs,' which occur in the skin of body and legs in several groups, is unknown.

The respiratory organs already alluded to (p. 443) have their spiracles, always few in number, on the anterior ventral part of the abdomen and, it is stated, sometimes on the cephalothorax. The internal organs are the lungs and the tracheæ. A lung is a rounded sac just inside the spiracle and consists of numerous leaves on the anterior wall of the lung sac. Each leaf is covered on each side by a thin layer of chitin and contains a blood space in its interior, while between the leaves are flattened spaces into which the air enters (fig. 456). The tracheæ, on the other hand, are branched tubes arising from the abdominal spiracles and penetrating the abdomen (fig. 460). These are lined with chitin, and to strengthen them without undue thickness this lining is thrown into folds, usually arranged in a spiral. In the scorpions and tetrapneumonous Araneina only lungs occur. In other spiders one pair of lungs is replaced by tracheæ, while in most other arachnids only tracheæ occur. (The smaller mites and parasites lack specialized respiratory organs and circulatory organs as well.) These facts, aside from embryological conditions, show that lungs and tracheæ are morphologically equivalent. The localization of respiration in the abdomen has resulted in having the heart in the same region. It is noticeable that, as the tracheæ are developed, the circulatory vessels are reduced. In the scorpions, which have only lungs, the circulation is most nearly complete.

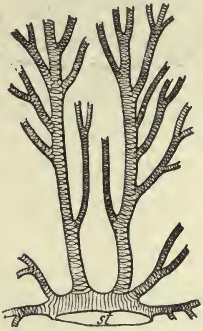


Fig. 460.—Beginning of paired tracheæ of *Anyphæna accentuata*. (After Bertkau.) *st*, unpaired spiracle.

In development the arachnidan tracheæ arise from the abdominal appendages, as do the lungs. (In the Solpugidæ and some mites cephalothoracic tracheæ occur, but nothing is known of their development.) This fact shows that they are entirely different in origin from the tracheæ of insects, while numberless details show that these structures are only to be compared with the gills of Limulus.

The gonads (only the Tardigrades are hermaphroditic) are abdominal in position and open by paired ducts (sometimes with a single mouth) on the first abdominal somite. In most cases the animals are oviparous, but the scorpions and many mites bear living young. In many instances the mothers care for their eggs and young, the scorpions carrying their families on their bodies. Only rarely is there a metamorphosis, and then in the aberrant forms like the Linguatulida and Acarina, where the young have but two or three pairs of appendages, acquiring the others later.

Legion I. Arthrogastrida.

Arachnida in which the abdominal somites are distinct.

Order I. Scorpionida.

The scorpions bear a superficial resemblance to crayfish and for a long time were associated with them, since (fig. 402) they have four pairs of walking feet (3–6), while the pedipalpi (2) are large and bear pincers. The cheliceræ are also chelate. The pedipalpi and the two anterior pairs of legs have the basal joint expanded for chewing. The peculiarities of the abdomen mark the group off from all other arachnids. It consists of seven broader somites attached by their whole width to the cephalothorax and behind six narrower somites, forming a tail or postabdomen. The last somite is bent ventrally in a sharp spine and contains two large poison glands. It is the 'sting' of the animal, which, in the case of the small species, causes painful wounds in man; and in the large tropical species is, perhaps, fatal. Usually scorpions feed upon insects, which they seize with the pincers, and, arching the tail over the back, kill with the sting. On the ventral surface of the second abdominal somite (fig. 461) are a pair of appendages, the combs or pectines; rods with teeth on one side of uncertain function. They are clearly appendages with modified gill leaves, and from their nearness to the sexual opening and their rich nerve supply are supposed to be stimulating organs in copulation. The

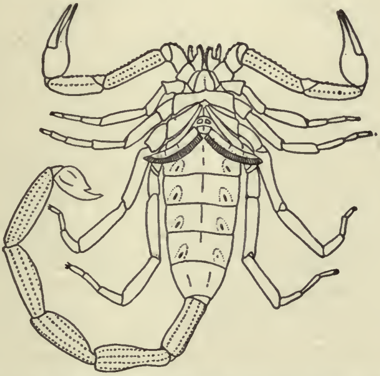


Fig. 461.—Under surface of scorpion, showing the combs and the outlines of the lung sacs with their spiracles (orig.).

next four segments bear spiracles which lead to four pairs of lung sacs. The heart is abdominal and the 'liver' diverticula are confined to the same region. The large number of abdominal ganglia distinct from the œsophageal ring is also characteristic. From three to six pairs of eyes occur.

The scorpions are inhabitants of warm regions, ranging north with us to the Carolinas and Nebraska. *Buthus*,* *Centrurus.**

Order II. Phrynoidea (Pedipalpi, Thelyphonida).

The thoracic segments are fused, and of the appendages only the last three are walking feet, the third pair having the last joint (tarsus) developed into a long many-jointed tactile flagellum. The cheliceræ are strong and spined, but end in a claw, not in a pincer. The cheliceræ are also clawed and are possibly poison organs, since the bite of these animals is feared. The abdomen consists of eleven or twelve somites and contains two pairs of lungs. There are eight eyes—two large ones in the middle of the cephalothorax, and three small ones on either side.

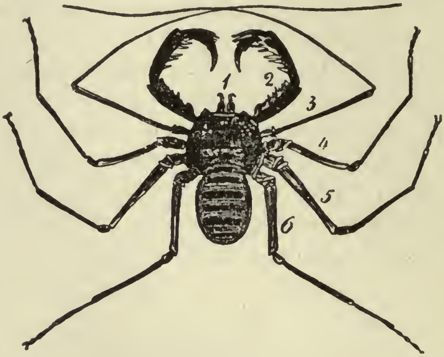


FIG. 462.—*Phrynus* (*Phrynichus*) *reniformis.* (From Schmarda.)

The species are tropical. *Phrynus* (fig. 462) has a simple abdomen; *Thelyphonus** (fig. 405, *D*) has a short postabdomen which bears a long, many-jointed thread. One species in the southwestern United States.

Order III. Microthelyphonida.

Small animals as yet known only from Texas, Sicily, Paraguay, and Siam. They have a general resemblance to a scorpion, the cheliceræ are three-jointed and chelate, the pedipalpi simple, neither these nor any of the legs having chewing lamellæ. The head is distinct from two 'thoracic segments,' the abdomen is eleven-jointed and is terminated by a long many-jointed caudal flagellum.

Lung sacs, which are true appendages without lung leaves, occur on abdominal segments four to six, and are eversible. The ovary is unpaired, the testes paired. There is a circumœsophageal nerve ring and a single abdominal ganglion. No Malpighian tubes occur. *Kœnenia.**

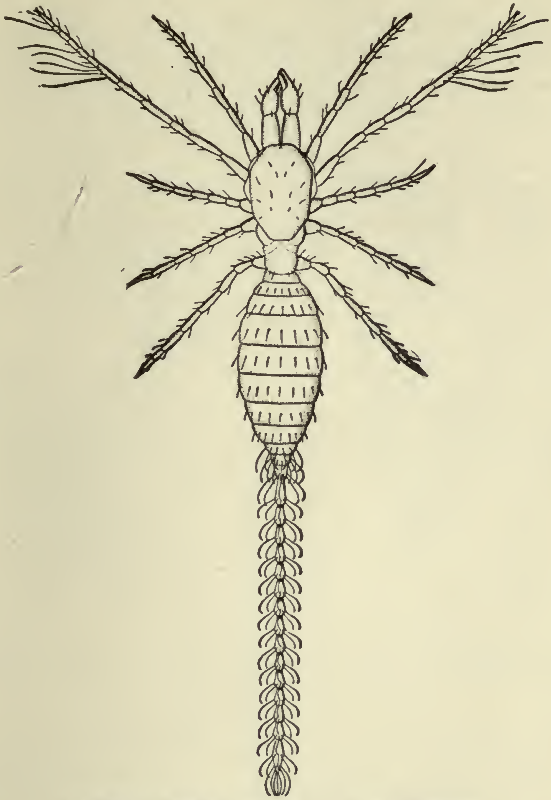


Fig. 463.—*Kœnenia wheeleri.** (From Wheeler.)

Order IV. Solpugida (Solifugæ).

In these the cephalothorax is broken up into a head bearing the cheliceræ, pedipalpi, and the first pair of legs; and three posterior free somites, each bearing a pair of legs, thus giving these forms a certain resemblance to the Hexapoda (*infra*). The cheliceræ are strong and chelate, the pedipalpi are simple and are used in walking, while the first pair of legs are tactile. Respiration occurs by four pairs of tracheæ, the first of which opens between the first and second 'thoracic' somites, a condition which deserves embryological investigation. The abdomen consists of nine or ten somites, and the head bears two ocelli.

As the name implies, the Solpugidæ are nocturnal, living by day in holes in the sand and searching for their prey at night. In the Old World they are reputed as poisonous, but no poison glands occur. Warmer parts of U. S. *Solpuga*,* *Galeodes*,* *Datames* * (fig. 464).

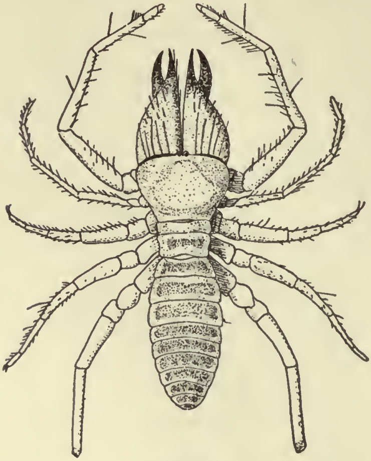


FIG. 464.

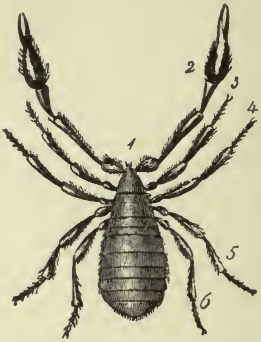


FIG. 465.

FIG. 464.—*Datames formidibilis.** (After Putnam.)
FIG. 465.—*Chelifer bravaisi.* (From Schmarda.) *1*, cheliceræ; *2*, pedipalpi.

Order V. Pseudoscorpii.

These small forms resemble the true scorpions in the chelate chelicerae and pedipalpi (fig. 465), and in the abdomen joined by its whole breadth to the thorax. They differ in the lack of post-abdomen and sting. They breathe by tracheæ; have from two to four ocelli, and spinning glands opening on the second abdominal somite.

These animals, 2–3 mm. long, live in moss, etc., and among old and dusty books, where they feed on mites and minute insects. Their bodies are flattened and they run sidewise. *Chelifer*,* *Obisium*,* *Chernes*.*

Order VI. Phalangida.

The abdomen in the harvestman, or 'daddy long legs,' is less evidently segmented than in the forms already mentioned, nor is it sharply distinct from the cephalothorax. The small body bears four pairs of exceedingly long legs; the chelicerae are drawn out in long horny processes; the pedipalpi are tactile organs as in the true spiders. The males possess a long penis, and the females a long ovipositor (fig. 466). They have two or four ocelli and breathe by tracheæ.

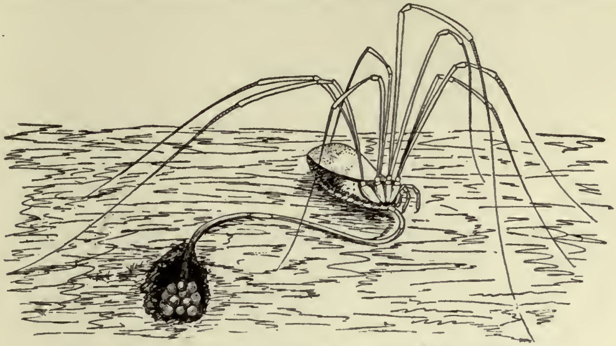


FIG. 466.—A phalangid laying eggs. (After Henking.)

These largely nocturnal animals are predaceous, feeding upon small mites. In structure they form in some ways an approach to the Acarina. *Phalangium*,* *Liobunum*.*

Legion II. Sphærogastrida.

Arachnida with the abdominal somites fused so that no traces of segmentation remain.

Order I. Araneina.

In the spiders the soft-skinned body is divided by a deep constriction into cephalothorax and abdomen (fig. 467). The four pairs of legs are adapted for springing or for walking, the hinder pair being also accessory to the spinning. It bears a comb-like claw with which several threads are combined into a stronger cable. The chelicera bears a sharp claw (fig. 459), traversed by the duct of the poison gland with which the prey is killed, although but few (species of *Latrodectes*, fig. 468, the tarantula, and the bird spiders, Mygalidæ) can injure man. The pedipalpi are used as feeling

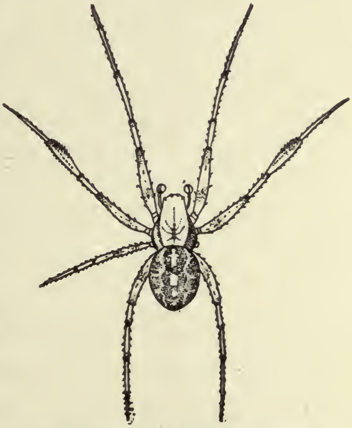


FIG. 467.—*Epeira insularis*,* round-web spider. (After Emerton.)

organs and with the basal maxillary process to comminute the food. In the male the pedipalpi have the terminal joint swollen to a pear-shaped structure (fig. 469) by which the sexes are easily distinguished. This is used to convey the spermatozoa to the female, a rather dangerous process, as the male is apt to be killed by the much stronger mate.

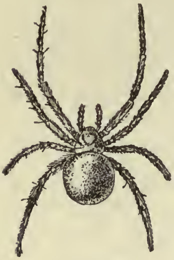


Fig. 468.

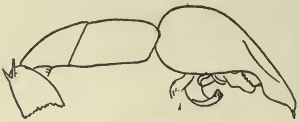


Fig. 469

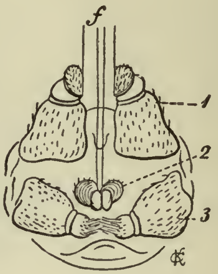


Fig. 470.

Fig. 468.—*Latrodectes mactans*,* poison spider. (After Marx.)
Fig. 469.—Pedipalp of *Pardosa uncata*. (After Emerton.)
Fig. 470.—Spinnerets of *Epeira diadema*. (After Warburton.) *1*, *2*, *3*, first, second, and third spinnerets; *f*, threads.

At the hinder end of the abdomen, just in front of the anus, are the *spinnerets*, which are reduced appendages, as is shown by their paired arrangement and their jointing (fig. 470), as well as by development. They are truncate and have at the tip a 'spinning field' from which numerous minute, two-jointed spinning tubes, resembling hairs, arise, each of which is the end of a duct of a silk gland. Different kinds of glands, producing silk for different purposes, occur. The number of spinnerets varies between two and three pairs, and in front of these may be an unpaired spinning region, the cribrellum, so that hundreds or even thousands (Epeiridæ) of glands may be present.

The secretion of the glands hardens in contact with the air, and the single threads are united by the combs of the hinder feet into a larger cord which can be regulated in size according to the number of glands which are active. Yet the largest cord is finer than the finest silkworm silk, hence it is often used for the cross-hairs of telescopes. The spider silk has many uses; it is used to line the nests, to form cocoons for the eggs, as a means of descent from high places, and to form the well-known webs.

The nervous system consists of a brain and a circumœsophageal ring, and, in the Mygalidæ, a single abdominal ganglion. The arrangement of the six or eight ocelli and the relative lengths of the legs are matters of systematic importance. Two pairs of respiratory organs occur. In the Tetrapneumones there are two pair of lungs, but in the Dipneumones the hinder pair are replaced by tracheæ, which may open by separate spiracles (Tetrasticta) or by a common opening (Tristicta, fig. 460).

Sub Order I. TETRAPNEUMONES. Four lungs, four spinnents and eight eyes in two rows. The MYGALIDÆ are the most important group, large forms which spring upon their prey, capturing even small birds and mice. To the genus *Mygale** belong the spiders (commonly but erroneously called tarantulas) which occur in banana bunches. Here also belong the trap-door spiders, *Cteniza*,* of the southwest, which excavate burrows in the soil, line them with silk, and close them with a hinged lid (fig. 471). *Atypus.**

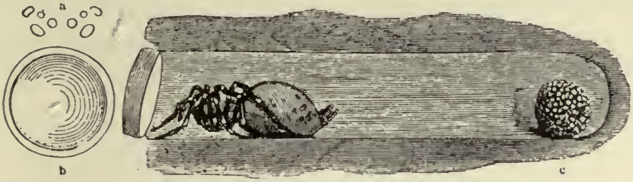


FIG. 471.—*Cteniza cæmentaria* in its tube, closing the lid. *a*, eyes; *b*, inside of lid with places for the claws; *c*, egg cocoon.

Sub Order II. DIPNEUMONES. One pair of lungs, one of trachea; six spinnerets. Here belong most of the native and numerous tropical species. Some (VAGABUNDÆ) use their webs only to line the nests and enclose the eggs, which are either hidden away or carried about attached to the body, while they spring upon or chase their prey. SEDENTARIA are the web builders, their webs varying widely in structure. Of the first group the SALTIGRADA include forms which jump upon their prey (*Attus*,* *Phidippus*,* *Habrocentrum**), and the CITIGRADA (*Lycosa*,* *Dolomedes*,* *Trochosa**), which run their prey down. Among these is the true *Tarantula*, *T. apuliæ* of Italy, whose bite was once believed to cause a frenzy only to be cured by peculiar music ('Tarantello'). The Sedentaria are divided according to the web-building habits. The ORBITELARIÆ or orb weavers (*Epeira*,* *Argiope**) form vertical webs which in many instances are complete circles. The RETITELARIÆ (*Theridium*,* *Erigone**) build irregular webs. The species of *Latrodectes** are reputed poisonous to man (fig. 468). The TUBITELARIÆ build horizontal webs with a tube to the margin in which they lay in wait for insects.

Order II. Acarina.

The mites, partly from parasitism, partly from other conditions of life, have become, in some instances, considerably modified. With the fusion of cephalothorax and abdomen the last traces of segmentation in the body are lost. Yet they retain the six pairs of appendages—four pairs of legs which at once distinguish them from the parasitic hexapods; and two pairs of mouth parts, modified into a sucking beak. This consists of a tube formed by the basal joints of the pedipalpi, in which the cheliceræ, either chelate, clawed, or stylet-like, play.

Since the mites are small and half or wholly parasitic, they are much simplified in structure. Frequently heart and tracheæ are lacking. The larva as it escapes from the egg lacks the last pair of legs and then closely resembles certain imperfectly segmented parasitic insects like the lice.

The red mites or TROMBIDIIDÆ and the water mites, HYDRACHNIDÆ (*Hydrachna*,* *Atax* *), are free-living in the adult condition, but parasitic as young. The IXODIDÆ or ticks (*Ixodes**), live in woods or on bushes, attack man and other mammals, burrowing beneath the skin, sucking the blood until they become enormously swollen and fall off. The much smaller males are attached to the females and take no food. *Argas persicus*, of eastern lands, with habits like a bedbug, is poisonous. The GAMASIDÆ are parasitic, species of *Gamasus* * occurring on beetles and *Dermanyssus** on bats. The ACARIDÆ include permanent parasites like *Sarcoptes scabei* * (fig. 472), the cause of the 'itch,' and the closely allied cheese mite. The follicle mite, *Demodex folliculorum*,* lives in the sebaceous glands of various mammals, including man (fig. 473).

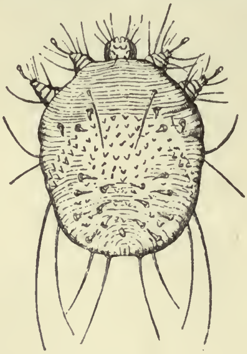


FIG. 472.

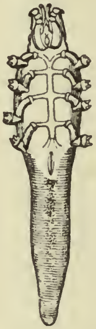


FIG. 473.

FIG. 472.—*Sarcoptes scabei*, female itch mite. (After Leuckart)
FIG. 473.—*Demodex folliculorum*, follicle mite. (From Ludwig-Leunis.)

Order III. Linguatulida.

Elongate mites like *Demodex* lead to the Linguatulida, which as adults live in the frontal sinuses of carnivorous mammals, as encysted young in the liver of herbivorous forms, especially rodents. The body is long, flattened and ringed, and hence somewhat tapeworm-like (fig. 112). The adults have the mouth at the base of a chitinous capsule, and on either side are two hooks regarded as the claws of the first and second legs. Inside the body is a spacious cavity traversed by the alimentary canal which is without appendages. The nervous system is largely a circumœsophageal ring; the sexual organs are very complicated, the males having the openings in front, the females at the hinder end.

The presence of these parasites in animals causes a profuse catarrh, and the eggs pass out with the mucus. Falling on vegetation, these are liable to be eaten by various animals. The larvæ (fig. 474) have a boring apparatus in front and two pairs of legs, the latter being lost in the metamorphosis except for the hooks. It is by no means certain that these are degenerate arachnids. The points in favor of such a position are about equally balanced by those against. *Pentastomum.*

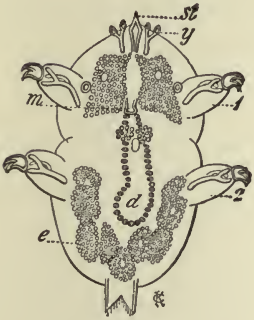


FIG. 474.

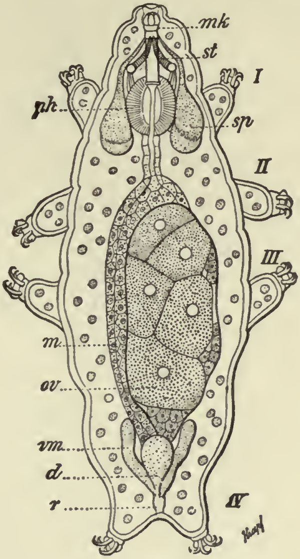


FIG. 475.

FIG. 474.—Larva of *Pentastomum proboscideum.* (After Stiles.) *d*, stomach; *e*, gland cells; *m*, mouth; *st*, stylet; *y*, posterior larval hooks; *1*, *2*, legs.

FIG. 475.—*Macrobiotus hufelandi*, water bear. (After drawings by Greef and Plate.) *I-IV*, legs; *d*, accessory glands; *m*, stomach; *mk*, mouth capsule; *ov*, ovary; *sp*, salivary glands; *st*, stylets; *vm*, excretory tubules; blood cells in the body.

Usually associated with the Arachnida are two other groups of very doubtful position, which until more definite knowledge is obtained, may remain near them.

Tardigrada.

These are minute fresh-water forms, known to microscopists as 'water bears' (fig. 475), which owe their name to their slow motions. They have four pairs of short, hooked legs, their sole Arachnidan character. The genital ducts empty into the rectum; the nervous system has four ventral ganglia; heart and respiratory organs are lacking. In development they are remarkable for the large cœlomic pouches. In the feet are glands recalling nephridia in their history. It is possible that these animals are to be placed among the Cœlhelminthes. *Macrobiotus.**

Pycnogonida (*Pantopoda*).

These marine animals have a cylindrical body, with a tubular proboscis in front and an abdominal appendage behind, and four pairs of very long legs. In front of the legs is a pair of small chelate appendages and usually a pair more like pedipalpi. In the male there is an additional pair of 'ovigerous' legs to which the eggs are attached after being deposited by the female, thus giving a total of seven appendages, a number not reached in any arachnid. Diverticula of the stomach extend into the legs; a heart is present, but respiratory organs are lacking. The Pycnogonids, which creep slowly over seaweeds and hydroids, may be (1) a distinct group of arthroproda, or (2) modified arachnids, or (3), and less probable, Crustacea. *Nymphon,** *Phoxichilidium,** *Colossendeis.**

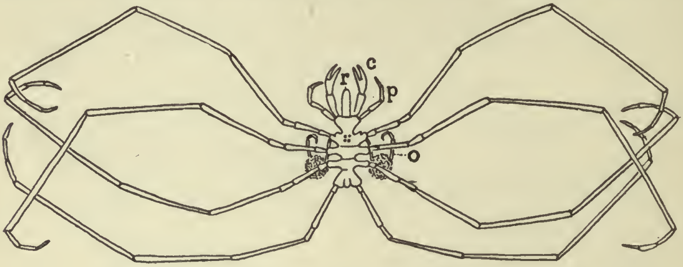


Fig. 476.—*Nymphon strœmii* * (orig.). *c*, cheliceræ ; *o*, ovigerous legs ; *p*, pedipalpi ; *r*, rostrum.

Class III. Malacopoda (Protracheata).

These forms, including only a single family PERIPATIDÆ, show a strange mixture of annelid and arthropodan (or 'tracheate') characters, so that they are usually regarded as representatives of the stock, early separated from the annelids, from which the Insecta have descended. They recall the annelids by the presence of nephridia, so characteristic of that group, which begin by a closed vesicle (reduced cœlom), pursue a short course, and expand into a urinary bladder before opening at the bases of the legs (fig. 478, *so*). On the other hand they possess tracheæ, long unbranched

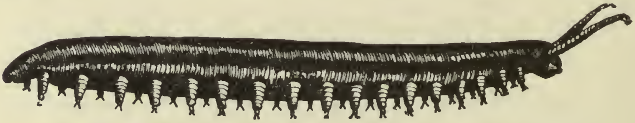


Fig. 477.—*Peripatus capensis.* (From Balfour, after Moseley.)

tubes which arise in numbers from the spiracles, which are irregularly distributed in each somite (fig. 478, *tr*).

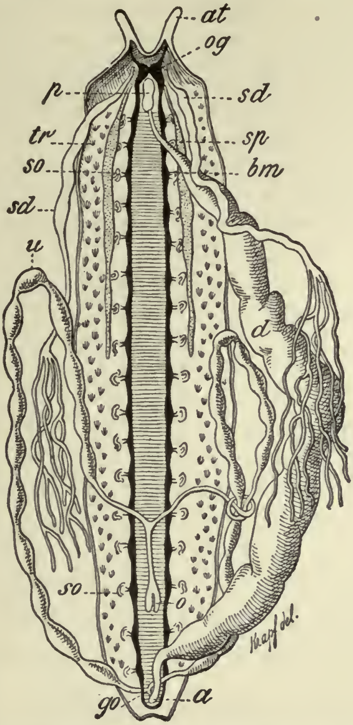


FIG. 478.—Anatomy of female *Peripatus* opened dorsally. (From figures of Moseley and Balfour.) *a*, anus; *at*, antennæ; *bm*, ventral nerve cords; *d*, digestive tract; *go*, genital opening; *o*, ovary; *og*, brain; *p*, pharynx; *sd*, slime gland; *so*, nephridia; *sp*, salivary gland; *tr*, tracheæ; *u*, uterus.

The soft-skinned body, which shows no external ringing, bears the legs, each terminated by claws. These legs somewhat resemble the annelidan parapodia in that they are not jointed and are not sharply separated from the trunk. Each segment bears legs, while the head is provided with three pairs of appendages: a pair of ringed antennæ, a pair of mandibles, which lie in the oral cavity, and a pair of mouth papillæ, at the tips of which are the openings of the slime glands, the sticky secretion of which is squirted out and serves to capture insects (fig. 478, *sd*).

The nervous system consists of a pair of cerebral ganglia (*og*), supplying the antennæ and a pair of very primitive eyes; and a pair of ventral cords (*bm*), swollen slightly in each segment, which connect dorsal to the anus and are connected in the trunk by numerous non-segmental commissures.

The description may be completed by saying that the straight alimentary canal (*p* and *d*) bears only salivary glands (*sp*); that it is accompanied throughout by a dorsal heart; that the gonads (the sexes are separate) open just in front of the anus (*go*), their ducts being modified nephridia. The animals are viviparous, live in decaying wood, hide by day and hunt their prey at night. The several species have a wide but discontinuous distribution (South America, Cape of Good Hope, New Zealand, etc.), an indication of great antiquity. Recently the forms have been divided into several genera, *Peripatus*, *Peripatopsis*, *Opisthopatus*, etc.

Class IV. Insecta.

The Insecta is a distinct group marked off from all other arthropods by several important characters. The appendages show no signs of a schizopodal condition. The head is always a distinct region, bearing a single pair of antennæ, a pair of mandibles, and two pairs of maxillæ, the posterior pair often being fused into a lower lip or labium.

The respiratory organs are *tracheæ* (figs. 479, 480), which resemble the trachea of

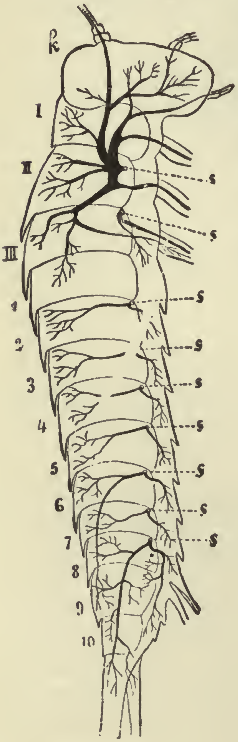


Fig. 479.

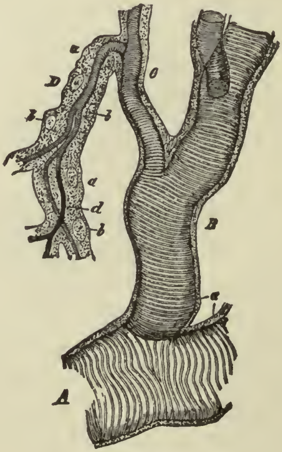


Fig. 480.

Fig. 479.—Tracheal system of *Machilis*. (From Lang, after Oudemans.) *k*, head; *I–III*, thoracic somites; *s*, spiracles; *1–10*, abdominal somites.

Fig. 480.—Portion of trachea of caterpillar. (From Gegenbaur.) *A*, main trunk; *B*, *C*, *D*, branches; *a*, epithelium with nuclei, *b*; *d*, air in tracheal tube.

man only in that they are tubes filled with air, and kept from collapse by firm walls. They open to the exterior by openings (*spiracles, stigmata*) on the sides of the body. They are inpushings of the skin and consequently have the same structure, an epithelium and an outer chitinous layer. The latter lines the lumen of the tubes, and since it must be thin to permit the passage of gases (oxygen, carbon dioxide), and at the same time firm, to keep the tubes open, it is thrown into folds which usually pursue a spiral course. The turns of the spiral are so close that it gives the tubes a ringed appearance. Inside the spiracles the tracheæ branch repeatedly until they end in the tissues in fine tracheal capillaries. In general it may be said that each segment has a right and a left spiracle and corresponding tracheal systems (fig. 59), but this scheme is complete in no known species, for there are always some segments (especially in the head) which lack these organs and are supplied from adjacent segments (fig. 479). Again, the tracheæ may be connected by longitudinal trunks (fig. 494, *tb*), so that spiracles occur in only a part of the segments, these supplying the whole system. Although the tracheæ are for aerial respiration, there are aquatic insects, but these also breathe air, since they carry air about with them entangled among the hairs which surround the spiracles. Then, too, aquatic larvæ often have tracheal gills, thin-walled processes of the integument which project into the water and are penetrated by numerous tracheal twigs (fig. 495).

The alimentary tract always has excretory organs, the Malpighian tubules, connected with it. These vary in number between wide limits, but are always placed at the junction of the rectum with the rest of the tract. They differ from the physiologically similar tubes of the Arachnida in being of ectodermal origin, so that no homology can be traced between them. The gonads are always paired and placed dorsal to the intestine, while the ducts (at least in some cases modified nephridia) open ventrally at the hinder end of the body. The spermatozoa are motile.

In the subdivision of the 'tracheate' arthropods a group of Myriapoda is usually recognized, containing forms known as centipedes and 'galley worms.' These two types are in reality very different. The centipedes (Chilopoda) show in all structural features close relationships to the Hexapoda, while the other group, Diplopoda, differ in almost every respect, except the presence of numerous walking legs, from the Chilopoda. Hence, since the object of classification is to show resemblances and differences, the group of Myriapoda has been dismembered, the Chilopoda being considered here, the Diplopoda as a distinct class at the end of the group of Arthropoda.

Sub Class I. Chilopoda.

The most striking characteristic of the chilopods is their long, flattened bodies, each of the numerous somites bearing a pair of six- or seven-jointed limbs. The head bears a pair of long antennæ and usually numerous ocelli, which only in *Scutigera* show a ten-

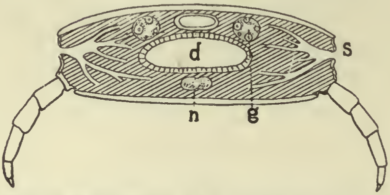


FIG. 481.—Diagram of transverse section of a centipede (orig.). *d*, digestive tract; *g*, gonad; *n*, nerve cord; *s*, spiracle and tracheæ.

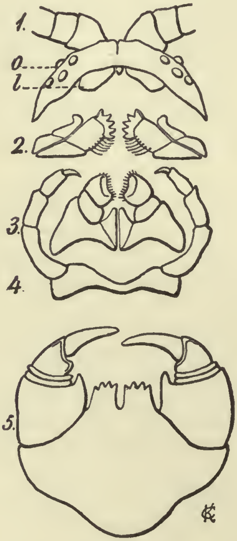


FIG. 482.

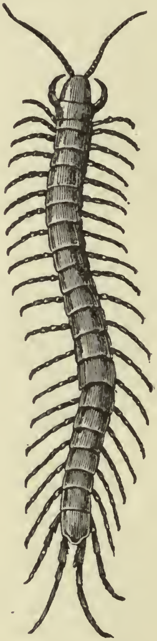


FIG. 483.

FIG. 482.—Mouth parts of *Scolopendra morsitans*. *1*, antennæ; *2*, mandibles; *3*, maxillæ; *4*, second maxillæ (labium); *5*, poison feet.
FIG. 483.—*Scolopendra morsitans*, centipede. (After Schmarda.)

dency to become compound. The mouth parts (fig. 482) are a pair of mandibles and two pairs of maxillæ, both united in the median line. Besides, the first pair of legs (fig. 482, *5*), with their fused bases, extend forward beneath the head and form the poison claws. Their terminal joints are sharp and contain the ducts of poison glands.

The spiracles (at least a pair to every other somite except those of the head) are lateral in position in the soft integument between the dorsal and ventral plates (fig. 481). The heart is elongate, with chambers in each somite (fig. 66); there are two large Malpighian tubes, and the nervous system is elongate, with ganglia in each somite. The gonads are dorsal to the intestine and are unpaired, while the single duct opens ventrally in the preanal somite.

The LITHOBIIDÆ, with 15 leg-bearing somites, have certain dorsal plates enlarged and overlapping the succeeding somites; *Lithobius*,* common under stones, etc. SCOLOPENDRIDÆ, centipedes; at least 17 legs and 5 ocelli; *Scolopendra*,* in warmer regions (fig. 483). GEOPHILIDÆ, not less than 30 pairs of legs, spiracles 2 less than legs. *Geophilus*.* SCUTIGERIDÆ, legs very long, 15 leg-bearing segments, but only 8 dorsal plates. *Scutigera*.*

Sub Class II. Hexapoda.

The Hexapoda is by far the largest division of the Arthropods, since it contains at least ten times as many known species as all the rest. The number is so large that it cannot be given with accuracy; an estimate is 250,000. Since the tropics, which have not been exhaustively studied, are very rich in insects, it is conceivable that there are at least a million different species in the world. On the other hand great uniformity of structure exists, all adhering with great fidelity to plan of structure, regional divisions, and number of appendages under the most diverse conditions, so that the difference between the most extreme forms is far less than that in Crustacea or Arachnida. But while hexapods thus lose in morphological interest, they gain in their life relations, in the way that they are injurious or beneficial to man, in their breeding habits, and in their intellectual and social relations. From the evolutionary standpoint they show marked adaptations to environment, and the large number of species is only possible by taking advantage of every opportunity in nature.

Of systematic importance are the regional division of the body and the number and character of the appendages. In the body three regions are distinguished, often separated by marked constrictions: head, thorax, and abdomen. The number of abdominal somites, varies with the order and even with the family, ranging between eleven (in some larvæ and embryos twelve) in the Orthoptera and five in many Diptera. Each cuticular abdominal segment consists of two plates, tergite (dorsal) and sternite (ventral), united on the sides by a softer membrane which contains the spiracles. Head and thorax, on the other hand, have a constant number of somites. The thorax is plainly divided into three segments, *pro-*, *meso-* and *metathorax,* each composed of three elements, an unpaired dorsal portion, *notum;* a pair of lateral plates, *pleura;* and an unpaired ventral *sternum* (fig. 484). For simplicity one speaks of pronotum, mesosternum, etc., to indicate the portions of the separate segments. The head is a continuous capsule in which the following parts are recognized: in front and dorsal *clypeus* and *frons;* dorsal and posterior a *vertex* and an *occiput;* laterally *genæ,* ventrally a *gula.* The appendages show that the head is composed of at least four somites.

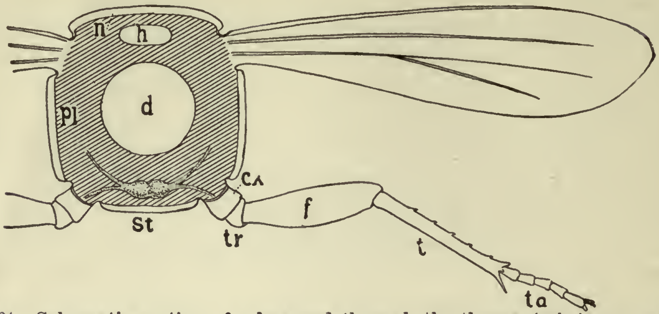


Fig. 484.—Schematic section of a hexapod through the thorax (orig.). *cx*, coxa; *d*, digestive tract; *f*, femur; *h*, heart; *n*, notum; *pl*, pleuron; *st*, sternum; *t*, tibia; *ta*, tarsus; *tr*, trochanter.

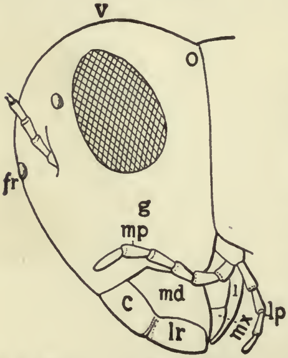


Fig. 485.—Head of a grasshopper. *c*, clypeus; *f*, frons; *g*, gena; *l*, labium; *lp*, labial palpi; *lr*, labrum; *md*, mandible; *mp*, maxillary palpi; *mx*, maxilla; *o*, occiput; *v*, vertex.

The view that the head consists of six somites is based on the existence of two more segments without appendages in the embryo, a preantennal and a postantennal (intercalary, premandibular), as well as the knowledge that the brain, in which formerly only antennal ganglia were recognized, consists of three pairs of ganglia (proto-, deuto-, and trito-cerebrum).

The appendages (fig. 484), seven pairs, are confined to the head and thorax (see, however, *infra*). The three thoracic segments bear three pairs of legs, whence the name Hexapoda. The legs are inserted between pleura and sterna and begin with a short coxa (*c*), followed by a trochanter (*tr*), also short. The two following joints are long, the first, the femur (*fe*), being large and containing the muscles; the next, tibia (*t*), being more slender; the foot, or tarsus (*ta*), is composed of a series of joints, the last bearing a pair of claws.

The first of the cephalic appendages, the antennæ, are the most leg-like, but normally are never clawed. They spring from the frons above the mouth and are innervated from the brain. The number and shape of the antennal joints varies with the group, and according as the single joints are lengthened or shortened, narrowed or expanded, or provided with appendages, etc., different kinds of antennæ—knobbed, club-shaped, toothed, feathered, etc.—are recognized, distinctions of great value in classification.

The morphology of the three pairs of mouth parts, the mandibles (*md*), maxillæ (*mx*), and second maxillæ, or labium (*la*, figs. 486–489), is more interesting. The labium, formed of united right and left appendages, lies behind the mouth and forms the lower lip, and is in contrast to the upper lip, or labrum (*lr*), which, however, is not appendicular in character. Both labium and labrum may bear unpaired processes on their oral surfaces, an epipharynx above, a hypopharynx below the mouth, neither of them true appendages.

The different kinds of food necessitate differences in the character of the mouth parts,—chewing, licking, sucking, or piercing—all referable back to the chewing kind, and these in turn are modified legs. In the description of the chewing type it is well to begin with the *maxillæ* (fig. 486), because of their easy comparison with the other mouth parts and with the legs as well. These begin with a triangular joint, the *cardo* (*c*), which is followed by a larger *stipes* (*st*). The stipes in turn supports two chewing lobes, the inner, or *lacinia* (*li*), and an outer, or *galea* (*le*), these being processes segmented off from the stipes. In the Orthoptera and Coleoptera only the lacinia is sharp-pointed ; the galea may either form a sheath for the lacinia, or, as in many beetles (fig. 514), it may be tactile and jointed again. The stipes also bears the maxillary palpus (*pm*), consisting of from three to six similar joints, and is the mostly leg-like part of the appendage.

The *labium* arises as a pair of processes which early approach each other and fuse behind the mouth. All the parts of the maxilla may be recognized, only it must be remembered that the basal parts of the two sides are fused. The united cardines form an under chin, the *submentum,* the stipites a chin or *mentum,* which in the Orthoptera is cleft, a result of incomplete fusion. This may bear inner and outer processes, the *glossæ* (*gl*) and the *paraglossæ* (*pg*) respectively, and the labial palpus. The *mandible* consists of merely the basal joint, altered for biting, while the rest of the appendage, common in crustacea as the mandibular palpus, is lacking.

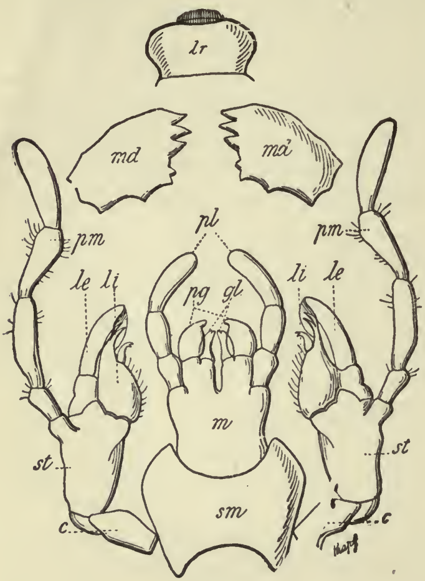


FIG. 486.

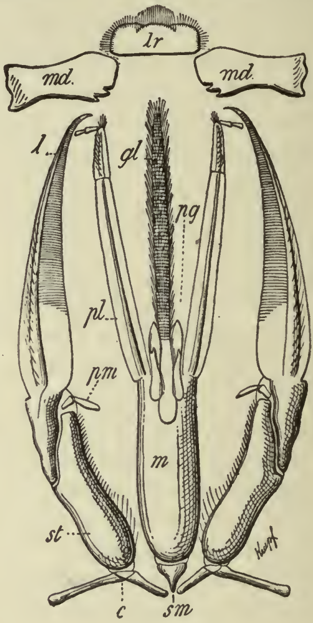


FIG. 487.

FIG. 486.—Chewing mouth parts of cockroach (*Periplaneta orientalis*). The lettering is the same in figs. 486–489. *c*, cardo; *gl*, glossa; *hy*, hypopharynx; *l*, lobe; *le*, *li*, external and internal lobes of maxilla; *lr*, labrum; *m*, memtum; *md*, mandible; *mx*, maxilla; *p*, *pm*, maxillary palpus; *pg*, paraglossa; *pl*, labial palpus; *sm*, submentum; *st*, stipes.
FIG. 487.—Licking mouth parts of bumble bee (*Bombus terrestris*).

The licking mouth parts, like those of the bees (fig. 487), stand next to those already described, there being many transitional stages. Labrum and mandibles retain their primitive condition, while maxillæ and labium are greatly elongate, are connected at the bases, and can be folded away beneath the head or extended at will. The small submentum is followed by an elongate mentum which bears the unpaired tongue or glossa (*gl*), which corresponds to the fused glossæ (or to the hypopharynx?) of the first type and which is used for sucking honey and hence has the form of a nearly closed tube. Beside it lie the rudimentary paraglossæ (*pg*) and the well-developed palpi. Similarly the maxillæ have small cardines and palpi, while the stipites and the undivided lobe (*l*) are long and well developed.

The piercing mouth parts of the flies (Diptera) and bugs (Rhynchota) can be compared with those of the bees in so far as the labium forms the groundwork of the whole (fig. 488). The beak (*rostrum, haustellum*) of these animals corresponds to the labium; it is a grooved structure, either fleshy and flexible, or stiff and jointed. The edges of the groove are inrolled so that there remains a narrow dorsal slit, which can be closed by the slender upper lip (*lr*). The tube formed of these parts contains four stylets, toothed or with retrorse hooks at the tip. These are the

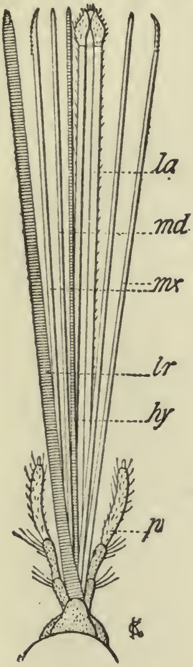


FIG. 488.

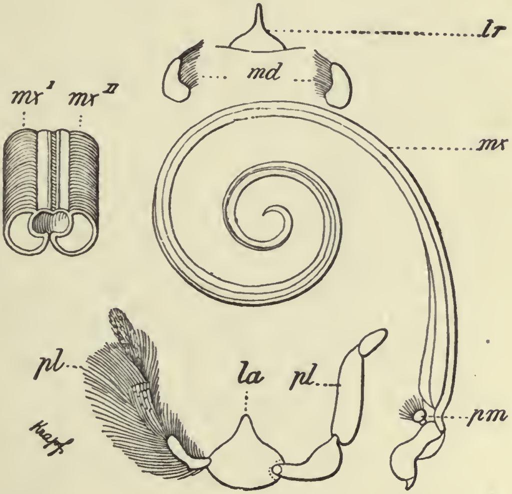


FIG. 489.

FIG. 488.—Sucking mouth parts of mosquito, *Culex pipiens.* (After Muhr.) The groove of labium opened by removing labrum; the stylets separated.

FIG. 489.—Sucking mouth parts of a butterfly. (After Savigny.) *mx'*, *mx''*, shows how right and left maxillæ unite into a tube; right labial palpus (*pl*) with hairs removed.

mandibles and maxillæ, and a fifth stylet, the hypopharynx (*hy*) can be present. Palpi, which only occur in the Diptera, belong to the maxillæ (*p*). Reduction in number of stylets to four or three, or their complete absence (some flies), is brought about by fusion or by degeneration. The haustellum serves as a case for the sucking tube, which in the Rhynchota is formed by the united maxillæ, in the Diptera by labrum and hypopharynx.

The proboscis, or haustellum (the so-called tongue), of the Lepidoptera (fig. 489) is a long tube coiled like a watch spring beneath the head. It consists of two long grooved maxillary galea firmly united by their edges. The maxillary palpi are well developed in the moths; elsewhere they show all stages of reduction to complete disappearance. Labium and labrum are reduced to small triangular plates at the base of the proboscis, the labium bearing a pair of hairy palpi (*pl*). The mandibles are represented by small plates or bunches of hair. These conditions gain in interest when we remember that in the larva the mandibles are strong biting organs, while the maxillæ are small hooks, and the labium is better developed only in those parts connected with the silk glands, a beautiful example of relations of structure to life conditions.

In contrast to the other regions, the abdomen lacks appendages in the adults. Only in the lower group of Thysanura are small lobes present, behind and in the same line with the thoracic feet, which may be regarded as abdominal feet. Apparently, too, the appendages of the last segment, the stylets and cerci, are modified limbs, but the parts (gonapophyses) used in copulation and oviposition are different in character. False feet, or pro-feet, occur on the abdomen of the larvæ of the Lepidoptera and the Tenthredinidæ, but since these are fleshy unjointed processes, it is doubtful whether these are true abdominal limbs, like those of other Arthropoda, or are structures independently acquired.

Besides ventral appendages the insects usually have two pairs of dorsal outgrowths upon the meso- and metathorax, the wings. They are lateral folds of the chitinous coat of the notum and contain on their interior extensions of the blood sinuses and of the tracheæ, which are protected by thickenings of the chitin, causing the network of 'veins' or 'nervures' in the wing. Both wings may be elastic, flexible, and adapted for flight, or the hinder pair may alone partake of this character (true wings or alæ), while the first pair may be thick and parchment-like wing covers, or *elytra,* under which the true wings are concealed when at rest. When only the base of the wing is thus thickened hemelytra result. Between the origins of the anterior wings is frequently a chitinous plate, the scutellum, while between the hinder wings is a similar postscutellum. In many insects one pair of wings is lacking, the anterior pair being retained in the Diptera, the posterior in the Strepsiptera; these are clearly cases of degeneration. The entire absence of wings may occur from two causes; wings have apparently never been developed in some (primary lack of wings of the Apterygota), while there are others in which we must believe that wings once present have been lost, because nearly related forms—bugs, lice, etc.—have wings, or because certain individuals (male cockroaches, sexual ants and termites) are winged (figs. 506, 528, 529). The prothorax of all recent insects is wingless, but in some of the Archiptera of the coal period wing rudiments occurred on this somite.

As a result of differences in food the alimentary canal (figs. 490, 491) varies greatly. The ectodermal stomodæum begins with a pharynx, which in the sucking insects is a sucking apparatus with radial muscles. The œsophagus, which follows, may be widened to a crop (ingluvies), or it may have a cæcal outgrowth which in the butterflies may take the shape of a stalked vesicle (falsely 'sucking stomach'). Also ectodermal is the gizzard (*km*, *pv*), or proventriculus, the chitinous lining of which is toothed for grinding the food. The true stomach, of entodermal origin (*m*, *cd*), frequently bears blind sacs or gastric cæca (*ap*); in general it is short and its junction with the hinder ectodermal portion, the proctodeum, is marked by the entrance of the Malpighian tubules (vasa Malpighii, *vm*). The latter, excretory in function, arise from the proctodeal region. The latter is usually differentiated into a small intestine and a two-regional (colon and rectum) large intestine. The rectum may have enlargements called rectal glands. True glands, however, occur only at the beginning and

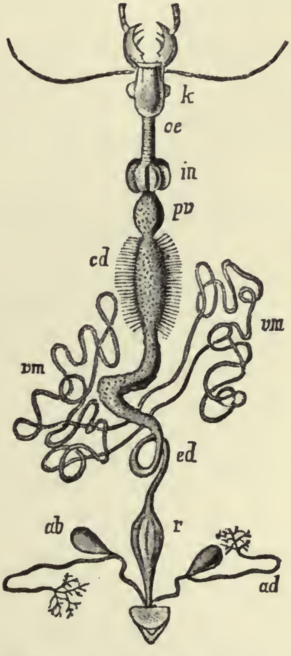


Fig. 490.—Alimentary tract of *Carabus auratus*. (From Lang, after Dufour.) *av*, anal vesicle; *ad*, anal gland; *cd*, stomach with cæca; *ed*, hind gut; *in*, ingluvies (crop); *k*, head; *oe*, œsophagus; *pv*, proventriculus (gizzard): *r*, rectum; *vm*, Malpighian tubules.

end of the alimentary tract; into the mouth empty from one to four pairs of salivary glands (*sp*); at the anus are defensive anal glands with their malodorous secretions of a protective character. The alimentary tract with the other viscera is enveloped in the fat body, a soft mass which contains, besides fat cells and connective tissue, concretions of uric acid.

The nervous system (fig. 405) has the ventral cord, especially in primitive forms (Apterygota, Archiptera, Orthoptera, fig. 491), and nearly all larvæ (fig. 59), long and composed of numerous separate pairs of ganglia. In beetles, moths, bees (fig. 494), and flies the cord is shortened and the ganglia are in part fused. The brain arises by the fusion of three pairs of ganglia (proto-, deuto-, and tritocerebrum), and is, especially in the adult, very complex. It is connected on either side with a large optic ganglion the size of which is correlated to that of the eyes. In the adult condition the Hexapoda have a single pair of highly developed compound eyes (figs. 407, 408), which not infrequently occupy nearly the whole of the top of the head. Between and in front of these small and simple ocelli, usually three in number, frequently occur, especially in insects which are strong fliers. These are either lacking or poorly developed in the larvæ, while the compound eyes are frequently replaced by groups of from two to six closely crowded ocelli. Of other sense organs only the tactile hairs of the skin are known with certainty, while similar hairs on the antennæ and about the mouth are supposed to be organs of smell and taste, since these senses are known to be well developed. The tympanal organs of the Orthoptera are the only structures which can be with

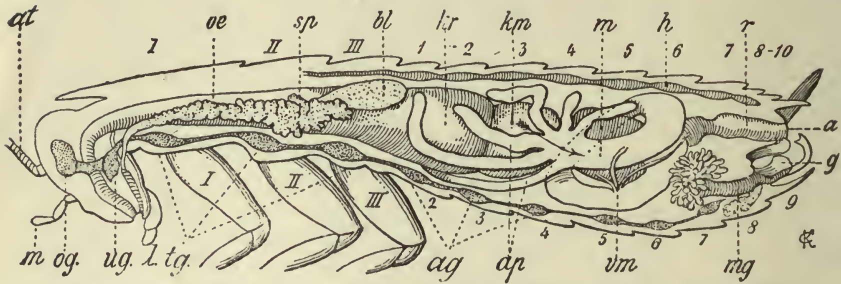


FIG. 491.—Viscera of male cockroach (*Periplaneta orientalis*). (Partly after Huxley.) *I–III*, segments of thorax and corresponding legs; *1–10*, abdominal segments; *a*, anus; *ag*, ventral ganglia; *ap*, gastric cæca; *at*, antenna; *bl*, salivary bladder; *g*, sexual opening; *h*, heart; *kr*, crop; *km*, gizzard; *l*, labial palpus; *m*, stomach (the arrow shows the connexion between *m* and *km*), also maxillary palpus; *mg*, male genitalia; *oe*, œsophagus; *og*, brain; *r*, rectum; *sp*, salivary gland; *tg*, thoracic ganglia; *ug*, infraœsophageal ganglion; *vm*, Malpighian tubules.

much probability connected with hearing. These are thin drum-like parts of the chitin, framed in thicker portions (figs. 492, 493), beneath which is a tracheal vesicle, with a nerve ending in a 'crista acustica.' The power of producing sound is widely distributed and often highly developed, the organs for this purpose varying widely in character. Stridulating organs are formed by ridges on wings and legs, which are rubbed against each other or against similar ridges on the body. Humming is produced by the action of the wings or by the passage of air through the spiracles, which are often provided with vibrating membranes which also serve to close these openings.

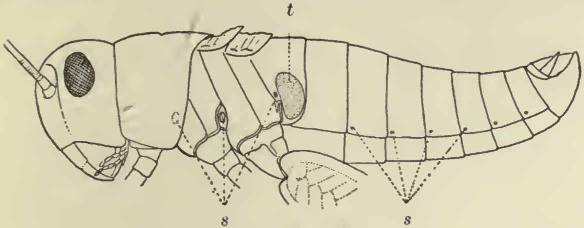


FIG. 492.

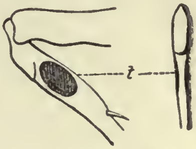


FIG. 493.

FIG. 492.—Side view of grasshopper. *s*, spiracles; *t*, tympanic organ.
FIG. 493.—Anterior tibia of a Locustid with tympanum, *t*. (From Hatschek, after Fischer.)

The tracheæ (figs. 479, 494) are usually united, just inside the spiracles, by longitudinal trunks from which fine branches extend, enveloping and penetrating all the organs with delicate silvery threads. This connexion of tracheæ renders it possible for the spiracles of some segments to disappear. The spiracles of the abdomen are the most constant, usually occurring in the soft membrane between the sternites and tergites; the thorax at most has but two pairs, the head none. In insects with good powers of flight many of the tracheal trunks are expanded to large air sacs, which may be of value as reservoirs of air, so that the ordinary respiratory motions are less necessary during flight.

An interesting adaptation of the tracheal system to aquatic life occurs in the larvæ of many Archiptera (Odonata and Mayflies) and Neuroptera, and even among Lepidoptera (*Paraponyx*) and Coleoptera (Gyrinidæ). The spiracles here are usually closed, and the taking of oxygen occurs either through the skin or by means of so-called tracheal gills—bushy or leaf-like appendages of the surface or the rectum, richly permeated by tracheal branches (fig. 495). In such cases the tracheal system has two portions, one which receives oxygen from and gives off carbon dioxide to the water; the other which supplies the tissues with oxygen and receives carbon dioxide.

Since the tracheæ, with their fine branches, supply the tissues directly with oxygen, the blood-vascular system is rudimentary. Directly under the back lies the elongate tubular heart in a special pericardial sinus. This is a part of the hæmocœle cut off from the gastric portion of this space by an incomplete partition in which, right and left, are the wing muscles (*alæ cordis*) of the heart. The heart receives its blood through lateral ostia (eight or fewer) from the pericardial sinus or (Orthoptera) through ventral openings from the large hæmocœle. The blood passes forward through an anterior aorta into the hæmocœle and thence back to the pericardial sinus. The arrangement of the viscera, fat bodies, and muscles gives a certain regularity to the circulation, especially in the appendages. Accessory pulsating ampullæ in the bases of

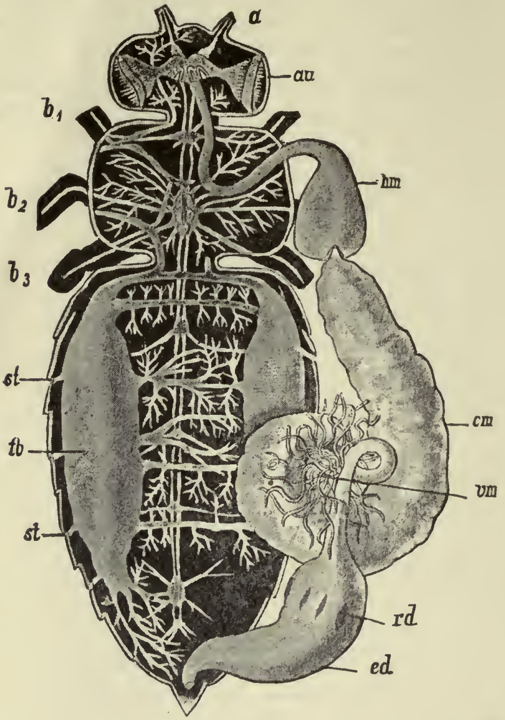


FIG. 494.

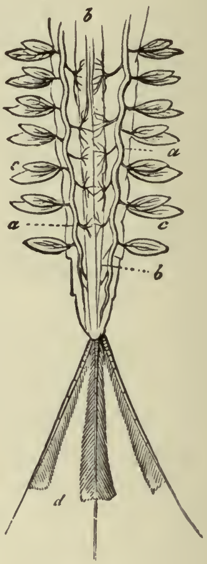


FIG. 495.

FIG. 494.—Anatomy of honey bee. (From Lang, after Leuckart.) *a*, antennæ; *au*, eye; *b*, legs; *cm*, chyle stomach; *ed*, rectum; *hm*, honey stomach (proventriculus), *rd*, rectal glands; *st*, spiracles; *tb*, tracheal chambers with tracheæ; *vm*, Malpighian tubules.

FIG. 495.—Abdomen of *Ephemera* larva (from Gegenbaur) with tracheal gills, *c*; *a*, tracheal trunks; *b*, intestine; *d*, caudal bristles (cerci).

the antennæ (Orthoptera) help in the flow of the blood. It is noteworthy that many beetles (Meloidæ and Coccinellidæ) squirt blood through the jointing membranes of the legs as a means of protection.

The Hexapoda are diœcious. The gonads consist of a few or many ovarial or testicular tubules (figs. 496, 497), the latter sometimes coiled into small oval bodies. Ovaries and testes are paired and lie, right and left, in the abdomen. Their paired ducts (oviducts, vasa deferentia) open separately in the Ephemerida, but in all other Hexapoda there is a single ventral unpaired sexual opening just in front of the anus. This arises as a median invagination of the ectoderm (hence lined with chitin), which extends inwards and meets the genital ducts (modified nephridia), and forms the ductus ejaculatorius of the male, the vagina of the female. Aside from many accessory glands, the sexual apparatus shows the following differentiations: in the male vesiculæ seminales, as widenings or diverticula of the vasa deferentia; in the female the receptaculum seminis and the bursa copulatrix. The latter may be either the vagina or a blind sac arising from it, or a special invagination of the ectoderm, emptying into the vagina by an internal canal. It receives the penis. The receptaculum seminis, a stalked vesicle connected with the vaginia or the bursa, has a special biological interest. In insects which copulate but once during life it retains the spermatozoa for a long time—four years in bees—in a living condition. As the eggs are laid they are impregnated by sperma-

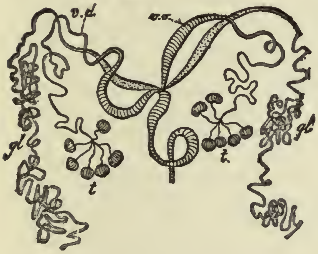


FIG. 496.

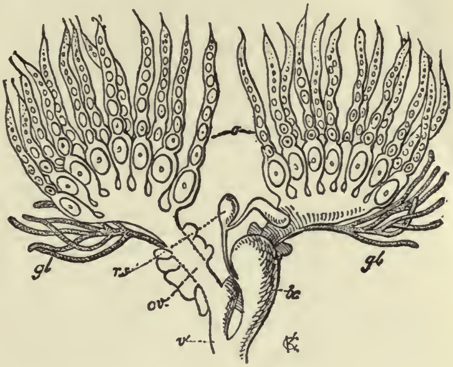


FIG. 497.

FIG. 496.—Male genitalia of *Melolontha*. (From Gegenbaur, after Fabre.) *gl*, accessory glands; *t*, testes; *vd*, vas deferens; *vs*, seminal vesicles.

FIG. 497.—Genitalia of female *Hydrobius*. (From Gegenbaur, after Stein.) *bc*, bursa copulatrix; *gl*, tubular glands; *o*, ovarial tubes; *ov*, oviduct with glands; *rs*, receptaculum seminis; *v*, vagina.

tozoa from it. Since a firm shell or chorion is developed around the egg in the ovary, access of spermatozoa is only possible by the existence of a micropylar apparatus, a system of tubes penetrating the chorion at one end of the egg.

Oviposition occurs in many insects by means of an ovipositor which may project free from the body (fig. 509) or may be retracted into it. It consists of four or (Orthoptera) six parts or gonapophyses developed from the eighth and ninth abdominal segment, which form a tube. In many Hymenoptera this structure has become modified into a sting (*aculeus*), and is provided with poison glands, making it an efficient weapon of defence. From its nature the sting is of necessity confined to the females. In the males there is usually a protrusible penis which is frequently composed of the same parts as the ovipositor; in others of metamorphosed somites. Further sexual differences lie in the form of the antennæ, shape and color of the wings, modifications of the eyes, etc.

In many insects the eggs may develop parthenogenetically. Plant lice and scale insects reproduce for generations asexually, and parthenogenesis is widely distributed among Hymenoptera, Lepidoptera, and Neuroptera. The conditions among the bees are especially interesting, since here the determination of sex rests with the existence or non-existence of fertilization (pp. 142, 487). Much rarer than the ordinary parthenogenesis is that special form, known as pædogenesis, which occurs only in certain Diptera like *Miastor*. In the female *Miastor* larva (fig. 498) the eggs develop before the appearance of the ducts, so that the young can only escape by rupture of the mother. After several pædogenetic generations there appear at last larvæ which pupate and produce adult male and female flies.

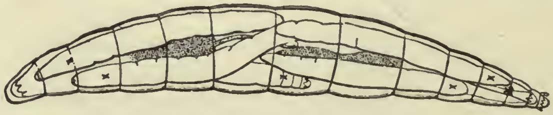


FIG. 498.—Larva of a Cecidomyid with pædogenetic daughter larvæ. (From Hatschek, after Pagenstecher.)

With the exception of these pædogenetic forms, the Pupipara, many Aphidæ and a few other viviparous species, the Hexapoda are oviparous. The development begins, after oviposition, by a superficial segmentation of the egg. Later there appear two embryonic structures, the yolk sac and the amnion; the first, in contrast to the vertebrate structure with the same name, is dorsal.

The amnion is a thin layer of cells which covers the ventral surface and arises in a manner similar to the vertebrate amnion; folds arising from the blastoderm in front and behind, right and left of the embryo, fuse with one another and produce a double envelope, an inner amnion, an outer serosa.

With the rupture of the amnion and egg shell, the postembryonic development begins. This differs so in the different orders that ametabolous, hemimetabolous, and holometabolous insects are recognized, *i.e.*, insects with direct development without metamorphosis, those with partial and those with complete metamorphosis. The ametabolous young is closely like the adult, so that it only has to grow, with periodic ecdyses, and to mature its reproductive organs. Since no insect has wings when it leaves the egg, this direct development is possible only in wingless forms like the Apterygota and Aptera.

All winged insects, on the other hand have a more or less pronounced metamorphosis, the final cause of which is the necessity of developing wings. This view holds although there are wingless insects with a complete metamorphosis. These forms (fleas, wingless moths, and ants) have undoubtedly sprung from winged species and have inherited from them the metamorphosis which has been retained after the wings were lost. In incomplete metamorphosis the differences between the newly hatched young and the adult, or imago, gradually disappear (fig. 499). At the second molt the wings often appear as small folds in the chitinous wall of meso- and metathorax; they grow with each ecdysis, until at last, in size, form, and movability, they are functional wings. The chitinous coat of each wing pad (fig. 499, *B, 1, 2*) encloses the compressed and folded wing of the next stage. Since the larvæ by their lack of wings are placed in different circumstances from the adult, the differences between the two may be increased by the development of special larval organs. Thus the aquatic larvæ of the May flies and dragon flies differ from the adults not only in the absence of wings, but by the different form and the tracheal gills, which are almost always lost at the last molt (fig. 495).

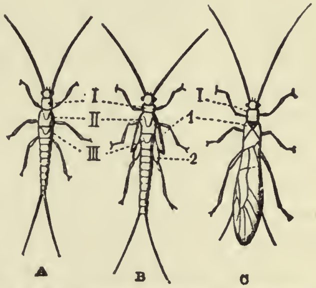


Fig. 499.—Hemimetabolous development of *Perla nigra*. (From Huxley.) *A*, wingless larva; *B*, larva with wing pads, *1, 2*; *C*, adult; *I, II, III*, thoracic segments.

Increase in the differences of environment and the correlated increase in larval characters lead to complete metamorphosis. In order to profit as much as possible by its adaptation to its environment the larva retains its shape as long as possible; the gradual change is suppressed and the alteration in form necessary to the metamorphosis is postponed until the end of the larval life, to the period between the last two molts. In this interval there is such an energetic transformation of the organism that the performance of ordinary vital functions, especially motion and feeding, is interfered with or rendered impossible. This last stage therefore becomes a period of rest, the pupal stage, upon the existence of which great weight must be laid in the definition of complete metamorphosis. The more complete the condition of rest the more pronounced is the holometabolous development. From this point of view different types of pupæ are distinguished: pupæ liberæ, pupæ obtectæ, and pupæ coarctatæ. In a free pupa (pupa libera) the appendages stand out from the body (fig. 500), so that not only the segmentation of the body but the antennæ, legs, wings, and often the mouth parts of the imago are visible. Such pupæ have a certain power of motion, as, for instance, the pupæ of many Neuroptera and mosquitos, the latter rising and falling in the water. The covered pupæ (pupæ obtectæ) at the moment of pupation have free appendages which with the hardening of the chitin become closely appressed to the body, so that even by close inspection only indistinct contours can be seen (fig. 501). Motion is confined to bending of the whole body, as is familiar in the pupæ of moths and butterflies. The pupæ coarctatæ are without motion because here the pupa (in structure a pupa libera) is enclosed in a larger coat, the last larval skin (Muscaria).

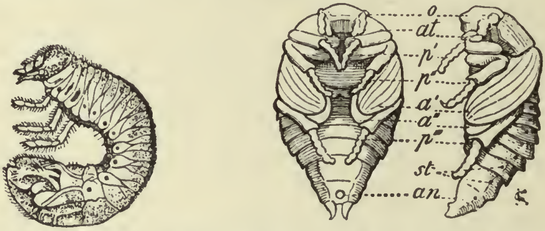


Fig. 500.—Larva and pupa of May beetle. a', a'', fore and hind wings; *an*, anus; *at*, antennæ; *o*, eyes; p'–p''', legs; *st*, spiracles.

The variations among larvæ are even greater than with pupæ. Here structure and jointing of the body are so completely under the influence of environment that with similar or different conditions larvæ widely remote from the systematic standpoint may closely resemble each other, while those of closely related species may differ extremely. The leaf-feeding larvæ of Lepidoptera (fig. 502) and Tenthreds are brightly colored, the thoracic appendages remaining small, and are reinforced by the fleshy ventral appendages, the prolegs or pedes spurii. The predacious larvæ of many beetles and Neuroptera have long thoracic legs, strong mandibles, and no prolegs. Other beetle larvæ, which burrow in wood or live in the earth (fig. 500), have plump whitish bodies, with the legs rudimentary or wholly lacking. These lead to the maggot-like larvæ, in which the mouth parts are inconspicuous and the distinction between head and thorax may vanish. Such soft-skinned annulated sacs occur in the bees (fig. 59) and other Hymenoptera, as well as in many flies (fig. 503); that is, in animals which live in an abundance of food either because of parasitism or because the mother has provided plenty.

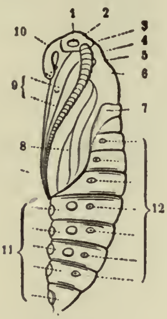


FIG. 501.

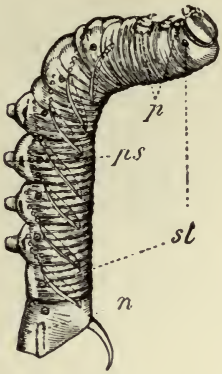


FIG. 502.

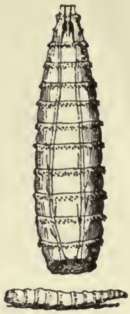


FIG. 503.

FIG. 501.—Pupa of *Sphinx ligustri*. (After Ludwig-Leunis.) *1*, eye; *2*, head ; *3*, antennæ; *4–6*, thoracic somites; *7*, hind, *8*, fore wing; *9*, legs; *10*, proboscis; *11*, abdominal somites; *12*, spiracles.

FIG. 502.—Larva of *Sphinx ligustri*. (After Ludwig-Leunis.) *n*, caudal disc; *p*, thoracic feet; *ps*, prolegs.

FIG. 503.—Larva (maggot) of blowfly, *Musca vomitoria*. (After Leuckart.)

From the outer appearance one would gain the impression that these holometabolous larvæ not only lacked the wings, but that the appendages of the imago were entirely absent or had an entirely different form; farther, that wings, and frequently antennæ, legs, and mouth parts, come into existence at the moment of pupation, and then in remarkable size and completeness. A more accurate investigation shows that the anlagen of all these structures are formed long before pupation, often at the first molt. The wings of a butterfly are present in the caterpillar as small folds or processes of the surface which increase in size with each molt. That they are not visible externally is due to the fact that they are pushed into the body and enclosed in sacs opening to the exterior. Such anlagen are called imaginal discs; with their recognition the distinctions between complete and incomplete metamorphosis in part disappear, since in the first the structures of the imago, even if in a modified shape, are outlined very early. Still there remains much to be remodelled during the pupal rest. The muscles must be adapted to the new locomotor organs, the digestive tract to the altered food, the nervous system re-formed. Since a great part of the previous structures must be broken down to afford material for the reconstruction of the organs, the pulpy nature of the inside of the pupa is easily understood. In a rapid degeneration of the tissues the material, consisting of indistinctly separated cells, is so homogeneous that it was formerly thought that the pupa returned to the indifferent condition of the egg (Histolysis of flies).

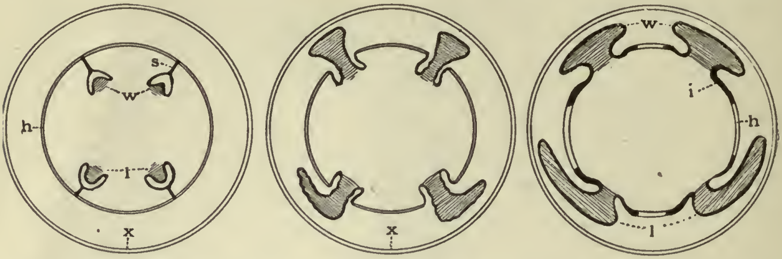


FIG. 504.—Diagram of development of wings and legs from the imaginal discs of a fly during metamorphosis. (After Lang.) *h*, larval hypodermis; *i*, imaginal hypodermis; *l*, *w*, imaginal discs and legs and wings formed from them; *s*, connexion of discs with hypodermis; *x*, chitinous larval skin.

In the classification four points are of special importance: (1) The segmentation of the body, in which it is to be noted whether the segments of thorax and abdomen follow without change of form, or whether the thorax, by the closer union of its somites, is sharply marked off from both head and abdomen. (2) The character of the wings, which are either lacking in the lower forms or are delicate chitinous structures, with numerous veins, the wings of the two thoracic segments similar. In the higher forms a degeneration of the wing veins or a leathery consistence of the membrane, together with a divergent development, partial reduction of antennæ and posterior wings may occur. (3) The structure of the mouth parts, and (4) the type of development, both described above. From these characters it is easy to differentiate six orders: Lepidoptera, Diptera, Aphaniptera, Rhynchota, Hymenoptera, and Coleoptera. The remaining forms were formerly divided among the Orthoptera and Neuroptera, but these groups are not considered natural and the attempt has been made to divide them into more or fewer groups. Here the Pseudoneuroptera or Aphaniptera are separated from the Neuroptera, the wingless forms or Apterygota from the Orthoptera.

Order I. Apterygota.

At the bottom of the Hexapoda come forms which lack wings and which show no evidence of having descended from winged ancestors. They are regarded as slightly modified descendants of the ancestral Hexapod. Besides the lack of wings they show many primitive characters; compound eyes are poorly developed or lacking; the tracheal system, when not degenerate, consists of isolated tracheal bushes, rarely connected by longitudinal trunks (fig. 479); the mouth parts, resembling somewhat those of Orthoptera, are for biting, though frequently rudimentary; the development is always ametabolous.

Sub Order I. THYSANURA (Bristle-tails). Body elongate, with long bristles (cerci) at the hinder end. *Lepisma saccharina*,* silver fish, common among old books and papers, does considerable damage. It is covered with shining scales. *Campodea** (fig. 400), with rudimentary abdominal appendages. *Machilis*,* *Iapyx*,* with caudal forceps.

Sub Order II. COLLEMBOLA (Spring-tails). Compressed forms in which the bristles bent under the body serve as a spring, throwing the animals (one to three mm. long) forwards. *Podura**; *Anurida maritima*,* in tide pools; *Entomobrya**; *Lipura**; *Achoreutes nivalis*,* the snow flea.

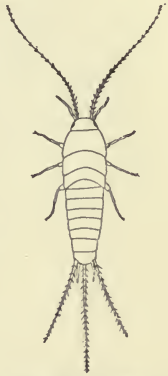


FIG. 505.—*Lepisma saccharina*,* silver fish. (After Packard.)

Order II. Archiptera (Pseudoneuroptera).

These represent the primitive forms of winged insects. The elongate body consists of numerous segments and usually bears the cerci of the Thysanura. The wings are delicate and transparent, supported by a close network of nervures, both pairs being very closely alike. The mouth parts are of the typical biting kind; the maxillæ have lacinia and galea; the labium, with glossa and paraglossa, is frequently deeply cleft. These points of primitive structure are correlated with a primitive, usually hemimetabolous development. The distinction between larva and imago is largely one of presence or absence of wings, although larval organs like gills (Amphibiotica) may occur. Frequently the development is direct when the imagines, as in some Termites and the Psocidæ, are wingless.

The Archiptera were formerly united with the Neuroptera on account of similarities of wings. The separation is due to characters of mouth parts and development.

Sub Order I. CORRODENTIA. Larvæ distinguished from the imagines by difference in size and, in the winged forms, by lack of wings. Best known are the TERMITIDÆ (Isoptera), or white ants, which must not be confused with the true ants (Hymenoptera), from which they are distinguished by the similar body segments, the mouth parts, and the simple development. Like the true ants, they have a well-developed social state. A colony of termites, consisting usually of thousands of individuals, forms a nest with numerous chambers and passages. They are nocturnal, and they burrow, without coming to the surface, through old wood (timbers of houses, furniture, picture frames, dead wood in the forest, etc.). They line these chambers with a cement-like substance composed of refuse which has passed through the alimentary canal. Many species build dome-like nests, ten or fifteen feet high, fifteen to twenty or twenty-five feet across, of chewed earth. In a colony are winged and wingless individuals, the latter with ametabolous development (fig. 506). The wingless forms have the sexual organs rudimentary, but, in contrast to ants and bees, may belong to either sex. They are frequently blind, have strong mandibles, and are of two kinds, the workers (*c*) and the large-headed soldiers (*d*). The winged forms are sexually functional (*b*). Shortly after the metamorphosis they swarm, and then the wings are bitten off at the base and 'king' and 'queen' either form a new colony or enter one already in existence. After copulation the abdomen of the queen, by the formation of numerous eggs, swells to an enormous size (*e*). Since the swarming individuals form the prey of birds and other animals, it often happens that a colony is left without a royal couple. In such cases the line is perpetuated by reserve males and females, sexual animals which have not com-

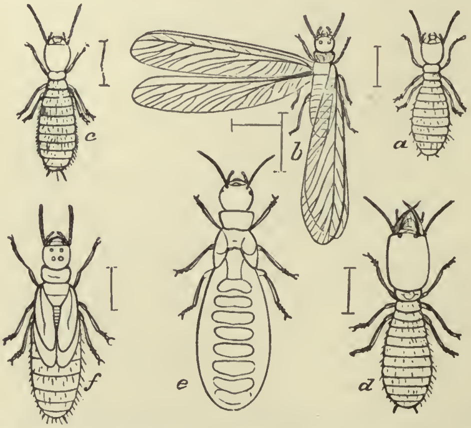


FIG. 506.—*Termes flavipes*,* white ant. (From Riley.) *a*, larva; *b*, winged male; *c*, worker; *d*, soldier; *e*, queen; *f*, pupa.

pleted the metamorphosis but are in the wing-pad stage. The termites are able, by quantity and quality of food, to modify the development of the larvæ and to determine which type of individual shall be produced. The termites are farther noticeable for the bitter wars they conduct against the true ants. *Termes flavipes** in our northern states. *T. fatalis*, Africa.

Allied to the Termites are the often wingless PSOCIDÆ, or book lice. *Troctes divinatorius** is the book louse. Other species are winged and live in moss, etc. Near here also belong the MALLOPHAGA, which, like lice, live upon mammals and especially on birds. Like true lice they are wingless, but they have biting mouth parts. *Trichodectes*,* on the dog, ox, etc.; *Goniodes*,* *Docophorus*,* *Nirmus*,* etc., on birds.

Sub Order II. AMPHIBIOTICA. The three families united here differ much in structure, but agree in having aquatic larvæ with tracheal gills (fig. 495). These are ventral bushes in the Perlidæ, wing-like or bushy appendages of the abdomen in the Ephemeridæ, and three-leaved appendages in those Odonata which do not respire by tracheal branches in the rectum. All of these larvæ are predaceous, especially the larvæ as well as the adults of the Odonata. The Odonate larvæ have a peculiar apparatus for the capture of prey. The mentum and submentum of the labium are greatly elongate and when folded bring the tip like a mask beneath the mouth. The structure can be suddenly extended (fig. 507) and grasps the food. PERLIDÆ (Plecoptera); hind wings the larger. *Perla*,* *Pteronarcys*,* stone flies. EPHEMERIDÆ, fore wings large, the hinder small or absent; May flies, life very short in the adult state. *Ephemera*,* (fig. 508) *Cleon*,* *Bœtisca.** ODONATA (Libellulidæ), wings nearly equal, the hinder slightly larger; Dragon flies, veritable insect hawks destroying numberless mosquitos. *Libellula*,* *Æschna*,* *Agrion*,* *Gomphus.**

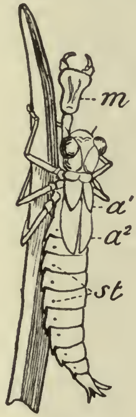


FIG. 507.

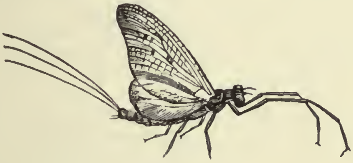


FIG. 508.

FIG. 507.—Larva of *Æschna grandis*. (After Rösel von Rosenhof.) a^1, a^2, wing pads; *m*, mask; *st*, spiracles.
FIG. 508.—*Ephemera vulgata*. (From Schmarda.) The caudal bristles incomplete.

Sub Order III. PHYSOPODA (Thysanoptera). Wings slender, fringed with hairs; tarsi bladder-like at tip; mouth parts bristle-like, probably used for sucking. The position of this group is very uncertain. *Thrips*,* *Limothrips.**

Order III. Orthoptera.

Like the Archiptera these are hemimetabolous or in a few cases ametabolous, and the mouth parts (fig. 486) are fitted for biting, the mentum being cleft. On the other hand the wings have lost the delicate membranous character and have become more parchment-like, the fore wings being smaller and serving as covers for the larger, softer, and folded hind wings, which are the efficient organs of flight; the condition in these respects recalling somewhat the Coleoptera. The abdomen bears cerci and frequently stylets. In internal anatomy the large number of Malpighian tubules is noticeable (fig. 491).

Sub Order I. CURSORIA. With rather long legs fitted for rapid running. Only the cockroaches (BLATTIDÆ) belong here. Wings may be absent, according to the species, in either sex, but more frequently in females. The more common cockroach, the 'Croton bug' (*Blatta germanica* *), is a well-known pest in houses. The larger *Periplaneta orientalis* * is common in ships and bakeries. Other species in our woods.

Sub Order II. DERMATOPTERA (Euplexoptera). Front wings short elytra; the hinder wings being folded crosswise and packed beneath them, or rudimentary; cerci developed to a forceps-like structure terminating the body, whence the name *Forficula* * given one genus. *Labidura.** These forms are often called earwigs, from an erroneous belief that they enter the human ear and injure the drum. The group on account of its wing structure is often made a distinct order.

Sub Order III. GRESSORIA. Legs long, slender, adapted to a slow walking motion. In the MANTIDÆ the prothorax is very long and bears a pair of long raptorial feet which when at rest are held in a position which causes these insects to be known as 'praying Mantes.' *Phasmomantis,** warm countries. PHASMIDÆ, with short prothorax, almost exclusively tropical, represented throughout northeastern United States by *Diapheromera femorata,** the walking stick. The members of this family are noted for their mimicry of twigs and leaves (fig. 12.)

Sub Order IV. SALTATORIA. Hinder legs long, strong, and for jumping; the other pairs much smaller. Hinder femora large and muscular, tibiæ elongate and spined. Wings usually functional and in the migrating species capable of sustained flight. Produce sound (stridulate) by rubbing the anterior wings together (Locustidæ, Gryllidæ) or against the legs (Acridiidæ). Tympanal apparatus (p. 468) on the anterior tibiæ (Locustidæ, fig. 493, and many Gryllidæ) or on the first somite of the abdomen (fig. 492). Stridulation occurs only in males, and in our common crickets the number of notes is directly dependent upon temperature, which, on the Fahrenheit scale, may be determined by the formula, $T = 50 + \frac{n - 40}{4}$, in which T stands for temperature and n for number of chirps per minute. The females may readily be recognized by the ovipositor. ACRIDIIDÆ; antennæ and ovipositor short; tympani abdominal. *Acridium*; Melanoplus** (*M. spretus*, the 'grasshopper' which did such damage in the Missouri River States in 1873–75); *Œdipoda*; Tettix.** LOCUSTIDÆ; antennæ long; tympani on first tibiæ; ovipositor long, flattened; tarsi four-jointed. *Hadenœcus*,* wingless, blind, in caves; *Conocephalus*; Cyrtophilus** and *Microcentrum*,* katydids; *Anabrus*,* wingless. GRYLLIDÆ, Crickets: antennæ long; ovipositor long, cylindrical; tarsi three-jointed; tympani on first tibia. *Gryllus*; Œcanthus*,* tree crickets; *Gryllotalpa*,* mole crickets, burrowing.

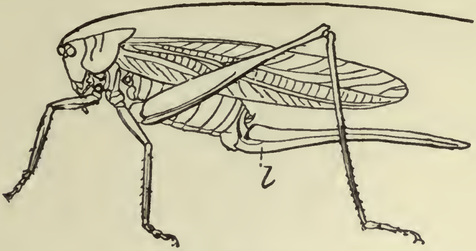


FIG. 509.—*Locusta caudata.* (After von Wattenwyll.) *l*, ovipositor.

Order IV. Neuroptera.

The Neuroptera closely parallel the Archiptera, and the two were formerly united, since they have the same wing structure and show in general appearance great similarities. Thus the ant lions (fig. 510) recall the dragon flies; the Chrysopinæ, the Perlidæ. The Neuroptera, however, are holometabolous and have a resting stage, although the pupæ (pupæ liberæ) are capable of some motion. The mouth parts are for biting, and in some the labium has no notch in the middle.

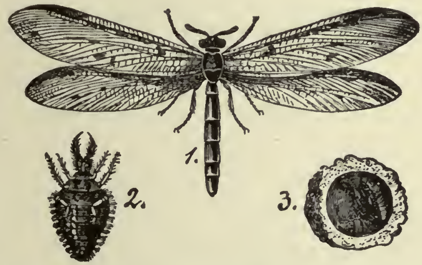


FIG. 510.—*Myrmeleo formicarius.* (From Schmarda.) *1*, imago; *2*, larva; *3*, pupa in its cocoon.

Sub Order I. PLANIPENNIA. Biting mouth parts. SIALIDÆ, wings well developed, mouth not rostrate, larvæ aquatic, commonly called dobsons. *Corydalis*,* hellgrammite; *Sialis*.* HEMEROBIIDÆ, lace wings; wings well developed, mouth not rostrate; larvæ with sucking mouth

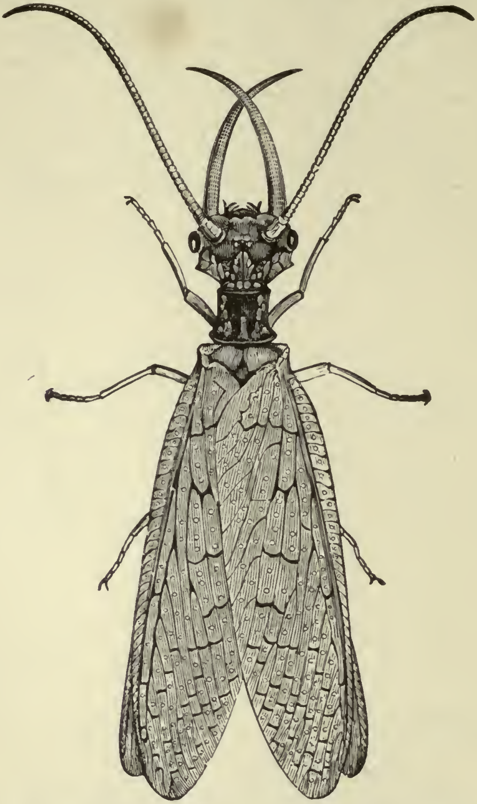


FIG. 511.—*Corydalis cornutus*,* hellgrammite, male. (From Riley.)

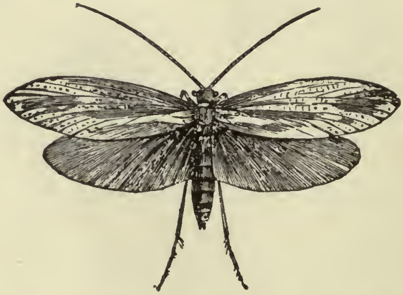


FIG. 512.—*Phryganea grandis*. (From Schmarda.)

parts, predaceous. *Chrysopa* * feeds on plant lice; *Myrmeleo*,* ant lions; larvæ dig funnel-like pits in sand and capture the ants, etc., which fall into them. PANORPIDÆ (Mecoptera); mouth prolonged into a rostrum; *Panorpa*, **Bittacus*.*

Sub Order II. TRICHOPTERA (caddis flies). Wings usually large; mouth parts rudimentary, forming a short sucking tube which, with the wings covered with hair-like scales, recalls the Lepidoptera; larvæ aquatic with tracheal gills; build cases of foreign matter, stones, sticks, etc., in which, like a hermit crab, they live; pupation occurs in these tubes. *Phryganea* * (fig. 512), *Hydropsyche*.*

Order V. Strepsiptera.

These forms, comprised in a single family, STYLOPIDÆ, are parasitic on the Hymenoptera. The six-legged larvæ (fig. 513, *3*) press in between the ventral abdominal plates of bees or wasps and pupate there. The quickly flying male (*2*) escapes from the pupal skin; it recalls somewhat a beetle; has small fore wings and large hinder ones. The wingless, legless female (*1*) remains in the pupal skin and is fertilized there; she is viviparous. Insects infested with these parasites are 'stylopized.' The affinities of the order are doubtful. The forms are frequently included with the beetles. *Stylops*,* *Xenos*.*

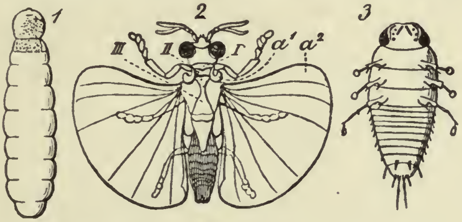


FIG. 513.—*Xenos rossi.* (After Boas.) *1*, female: *2*, male; *3*, larva; *I-III*, thoracic somites; a^1, rudimentary fore wing; a^2, hind wing.

Order VI. Coleoptera.

The beetles are the highest of the Hexapoda with biting mouth parts. They are closest to the Orthoptera, as is shown by the structure of mouth parts and wings. The mandibles are strong; the maxillæ (fig. 514) have lacinia and galea; the labium consists of a submentum (often called mentum), behind which the rudimentary mentum with its palpi, paraglossæ, and glossæ (the latter frequently fused to a ligula) are retracted. (In the genus *Nemognatha* the maxillary galea form a sucking organ.) The group is distinguished from the Orthoptera by the holometabolous development with pupæ liberæ, while the larvæ (fig. 500) show many modifications corresponding to the mode of lite. Another character is afforded by the wings. The anterior pair, separated at the base by a scutellum, are hard elytra not fitted for flight, and from these the order receives its name Coleoptera, sheath wings. Under the elytra are protected the delicate much folded hinder wings, the organs of flight (lacking in insects with fused elytra). Since the second and third thoracic wings and those of the abdomen are covered by the elytra, these are soft above. Externally the relations of the elytra cause a regional division peculiar to the beetles (fig. 515): head, prothorax, and a third division composed of meso- and metathorax plus abdomen covered by the elytra.

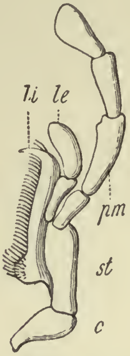


FIG. 514.

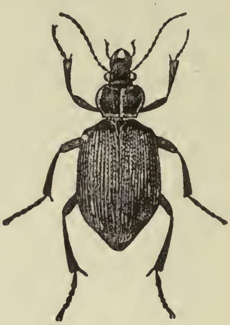


FIG. 515.

FIG. 514.—Maxilla of *Procrustes coriaceus.* c, cardo; *le*, galea; *li*, lacinia; *pm*, palpus; *st*, stipes.
FIG. 515.—*Calosoma sycophanta.* (After Ludwig-Leunis.)

The numerous species of beetles—over 100,000 are described—are subdivided into normal forms and Rhynchophora, the normal forms being subdivided again upon characters derived from the tarsi as follows:

Sub Order I. PENTAMERA. Tarsus five-jointed, the last club-shaped and bearing the claws, while the other four are short and somewhat heart-shaped (fig. 516, *a*). This is the largest division and contains the tiger beetles (CICINDELIDÆ) and the predaceous CARABIDÆ (fig. 515); the water beetles, HYDROPHILIDÆ and DYTISCIDÆ; the LAMELLICORNIA or SCARABEIDÆ, represented by the 'June bugs,' *Melolontha*,* and the large tropical *Dynastes;* the fire flies, LAMPYRIDÆ; the rove beetles, STAPHYLINIDÆ, etc.

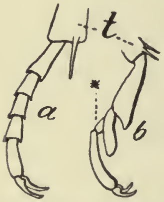


FIG. 516.—*a*, pentamerous tarsus of *Dytiscus;* *b*, cryptopentamerous tarsus of *Coccinella;* *t*, tibia; *, reduced tarsal joint.

Sub Order II. HETEROMERA. First and second legs pentamerous, third apparently four-jointed; few forms belong here, among them the 'oil bottles' (MELOIDÆ) and the blister beetles, CANTHARIDÆ, both of them containing a peculiar substance, cantharidin, which renders the Spanish flies, *Lytta vesicatoria*, an important ingedient of blistering plasters. Some of the TENEBRIONIDÆ live in the larval stages in flour, etc.

Sub Order III. TETRAMERA (Cryptopentamera). Tarsi with the penult joint rudimentary, giving the impression of four joints. The families included here, very numerous in species, are injurious to vegetation. The larvæ of the long-horned CERAMBYCIDÆ bore in wood. The CHRYSOMELIDÆ, of which the Colorado potato beetle (*Doryphora decemlineata*) is the most notorious, feed on leaves.

Sub Order IV. TRIMERA; tarsi with penult and antipenult joints rudimentary, so that they appear three-jointed. Best known are the COCCINELLIDÆ, or lady birds, whose larvæ, because of their destruction of plant lice, etc., are of value to man.

Sub Order V. RHYNCHOPHORA, snout beetles; head produced into a long snout, at the apex of which are the mouth parts. Here belong several families of weevils, some of which do damage to grain, nuts, timber, etc. *Curculio*,* *Conotrachelus*,* *Calandra*,* *Hylesinus*,* *Balaninus** (fig. 517).

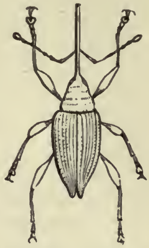


FIG. 517.—*Balaninus nasicus*,* hazel-nut weevil.

Order VII. Hymenoptera.

The Hymenoptera, of which bees, wasps, and ants are well-known representatives, have biting jaws, while the other mouth parts are elongate and in a minority of the group converted into a sucking organ. In the bees (fig. 487) the glossa unite, producing a nearly closed tube, which lies in a sheath formed by the other mouth parts, the mandibles alone retaining the primitive form. Since mouth parts vary, the structure of the wings and body segmentation have great value in defining the order. The wings are membranous and are supported by few nervures (fig. 518), and in flight they act as one pair, since the two are usually connected by hooked bristles on the hind wing, which engage in a groove on the hinder margin of the front wing. The fore wings are the larger and, correspondingly, the mesothorax exceeds the other thoracic somites, so that these, especially the prothorax, seem but parts of the strong mesothorax. Besides, the first abdominal ring unites to the thorax so intimately in the Entophaga and Aculeata as to seem part of it. The constriction which then separates thorax and abdomen comes between the first and second abdominal somites, and when the second (petiole) is elongate the stalked abdomen, familiar in the wasps, results.

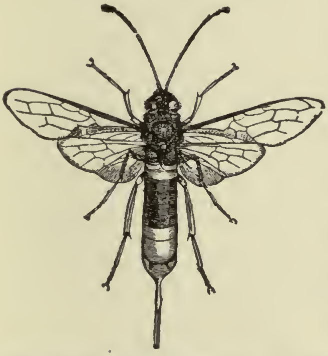


FIG. 518.—*Sirex gigas*, saw fly. (After Taschenberg.)

The sexes are readily distinguished by the genital armature. The female is provided with the ovipositor already described, which when used for this purpose only, projects from the hinder end of the body (fig. 518), but when used as a sting (aculeus), can be drawn back in the body when at rest. The sting, naturally lacking in the male, is connected with a poison gland, the secretion of which owes its effect, not, as once believed, to formic acid, but to a little known basic substance.

The distinction between ovipositor (terebra) and aculeus affords characters of systematic importance; others are furnished by the development, which is always holometabolous. The pupæ, in all important points, are similar (pupæ liberæ), but two kinds of larvæ are distinguished. Some have larvæ with well-developed legs; many of them are green in color and distinguished from the larvæ of Lepidoptera by the greater number of prolegs. Others have footless larvæ (fig. 59). The first occur where the larva must shift for itself, the second where it is surrounded by an abundance of food, either provided by the parents or by the host in which it is parasitic.

Sub Order I. TEREBRANTIA. Terebra present; larvæ with feet at least on the thorax; eggs laid on leaves or in wood, usually without gall formation; the larvæ therefore must move in order to feed. The TENTHREDINIDÆ, saw flies, feed on leaves and have caterpillar-like larvæ. *Cimbex*;* *Nematus*.* SIRICIDÆ (Uroceridæ), horn tails, the larvæ bore in wood and are whitish.

Sub Order II. ENTOPHAGA. Terebra present; larvæ legless, parasitic in galls or in animals. Some use the ovipositor to lay their eggs in leaves, roots, or stems of plants. Galls are then produced, diseased structures by which the larvæ are nourished. Others use the ovipositor to lay their eggs on or in other insects and larvæ. The young feed on the tissues of the host and at last cause its death, often before the completion of the metamorphosis. The gall-producing forms are the CYNIPIDÆ, some of which afford examples of heterogony (p. 145), in which the alternating generations are distinguished by different structure, by sexual and parthenogenetic reproduction, and by different kinds of galls. So different are the two generations that they have frequently been described as different genera. The inquilines do not form galls, but lay their eggs in the galls of other species. The insect parasites are divided among several families, the more prominent being the ICHNEUMONIDÆ, BRACONIDÆ, and CHALCIDIDÆ, those of the first being large, the others small or minute. These forms are of immense value to agriculture, as they keep down, as no economic entomologists or insecticides can, injurious forms.

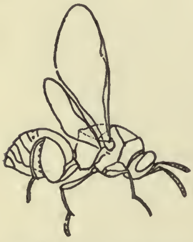


FIG. 519.—*Chalcis flavipes.** (After Howard.)

Sub Order III. ACULEATA. Females with stings; larvæ footless, maggot-like. The digger wasps or FOSSORES excavate tubes in the earth in which they lay their eggs and then bring into the holes as nourishment other insects which they have paralyzed by a sting in the ventral cord. Some true wasps have similar habits. Most wasps (VESPARIÆ) and bees (APIARIÆ) have different habits. They build wonderful homes of chewed wood (the first pulp paper) or skilfully trimmed leaves, earth, etc., or of wax which the animals (bees) secrete between the joints of the abdomen. The nests, which are to contain the young, are either small tubes or hexagonal cells which are united to horizontal or vertical combs; the food is either honey, pollen, or chewed fruits. The fact that the offspring are better protected when numerous individuals protect them has apparently led in the wasps and bees to different grades of social states. The honey bees (*Apis mellifica**), which live in a colony, consist of three kinds of individuals distinguished by structure of the head (fig. 520) and other features: a single queen, some hundred drones, and about ten thousand workers. These last are females and hence have stings, but have rudimentary functionless sexual organs; their work being to build the home, to protect the young, and provide food for the winter. The business of egg-laying belongs to the queen, who copulates but once, at the beginning of her reign, when she and a drone take a wedding flight. For the four years of her life the sperm retains its vitality in the receptaculum seminis. In laying the eggs she can permit entrance or not of the spermatozoa at will and thus produce males or females. A queen who has not been fertilized or who has exhausted her supply can only lay drone eggs. The further fate of the eggs depends upon the food of the larvæ; with a small amount of bee bread (pollen) workers are produced, but the same larva placed in a larger cell and fed with the 'royal jelly' (much like blanc mange in appearance) will develop into a sexually mature queen. On escape from the queen-cell the young queen with a part of the colony swarm and start a new colony. This operation may be repeated once or twice, but if there be danger of depleting the hive the remaining queen larvæ are killed. Wasps and bumble-bee colonies last but a year and are reformed by a fertilized female which has lived through the winter.

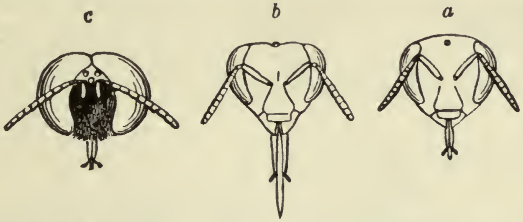


FIG. 520.—Heads of *Apis mellifica*. (After Boas.) *a*, queen; *b*, worker; *c*, drone with the compound eyes meeting above.

The ants (FORMICARIÆ) have gone beyond the bees in the social organization. They have also departed most from the other Hymenoptera in that the workers, sometimes the sexual individuals, are wingless and the sting is rudimentary or entirely lacking. Only the Poneridæ sting like bees and wasps; the others bite and squirt the secretion of the persistent poison gland (formic acid) into the wound. The homes of the ants are less wonderful than those of the bees, but their social organization is frequently more complicated. In the colony occur the wingless workers (rudimentary females with wing pads in larval life which are lost in pupation), and of these frequently there are different kinds, large-headed soldiers and small-headed workers; 'honey sacs' in *Myrmecocystus;* and the sexual animals, queens and drones, which copulate in a marriage flight. The queen after the flight returns to the colony. Frequently other insects, like the Aphides, are connected with the colony, these being kept for the honey dew they produce. Many ants steal the pupæ of others and keep the adults when they emerge as slaves. In *Polyergus rufescens* this has gone so far that the masters cannot care for themselves and must be fed by the slaves; otherwise they die. The ants possess extreme interest on account of their carefully planned wars (*Ecitons*); on account of their relations to plants, some species making nests in the growing plant and protecting it by their bites; the leaf-cutting ants take leaves from trees and carry them into their underground nests for the cultivation of fungi on which they feed; the agricultural ants from their plantations and stores of grain, and the honey ants from the fact that certain workers (fig. 521) act as reservoirs of honey, these 'honey sacs' swelling up to enormous size.

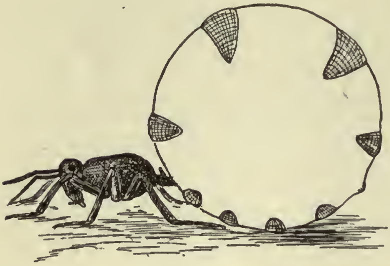


FIG. 521.

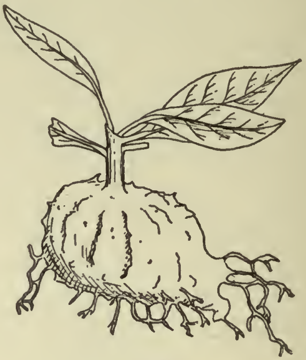


FIG. 522.

FIG. 521.—*Myrmecocystus melliger*,* honey-sac ant. (Orig.)
FIG. 522.—Plant of *Hydnophyton*. (After Forbes.) Showing the bulb occupied by ants.

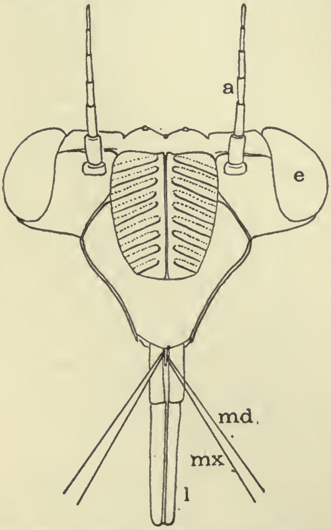


FIG. 523.—Head of *Cicada septendecim*, the mouth parts separated (orig.). *a*, antenna; *e*, compound eye; *l*, labium; *md*, mandible; *mx*, maxilla.

Order VIII. Rhynchota.

The Rhynchota, or bugs, in their external appearance are nearest to the Archiptera and Orthoptera. The head, thorax, and abdomen are joined in the same way; the development is hemimetabolous, and in the wingless species ametabolous. In some cases, as the Cicadas with their membranous wings, the confusion with the Orthoptera has led to these being called locusts; on the other hand the delicate-winged Aphides resemble the Archiptera. Yet all Rhynchota may be recognized by the sucking proboscis (fig. 523), consisting of the grooved labium in which the needle-like mandibles and maxillæ play. The wing structures afford the basis of division into three sub orders.

Sub Order I. HEMIPTERA (Heteroptera). Anterior wings hemelytra, *i.e.*, leathery at the base, soft and elastic at the tip (fig. 524); between the hemelytra is a conspicuous triangular scutellum (*s*) which covers more or less of the dorsal surface. Hemelytra and scutellum occasionally disappear. A further characteristic is the presence of stink glands, producing a most disgusting odor, which open in the adults ventrally on the metathorax; in the larvæ dorsally on the abdomen. According to habits the many families may be grouped into the aquatic HYDROCORES and the terrestrial GEOCORES. Of the first the BELOSTOMIDÆ are noticeable from their size, *Belostoma americana** being nearly 2½ inches long and capable of inflicting severe wounds. Other families are NEPIDÆ (*Ranatra*, water scorpion), NOTONECTIDÆ, HYDROBATIDÆ, etc. Of the Geocores the REDUVIIDÆ, which feed on other insects; the ACANTHIIDÆ (*Acanthia lectuaria*,* the bed bug); the LYGÆIDÆ, containing the chinch bug, *Blissus leucopterus*,* so injurious to grain; and the PENTATOMIDÆ, or stink bugs, may be mentioned.

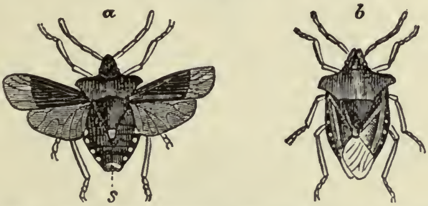


FIG. 524.—*Pentatoma rufipes*. (From Hajek.) *s*, scutellum.

Sub Order II. HOMOPTERA. Wings, when not degenerate, similar in texture throughout, although often differing in size. They are either parchment-like or delicate membranes. The CICADIDÆ, represented by *Cicada septendecim*,* the seventeen-year 'locust,' and *C. tibicen*,* or dog-day harvest fly, are noticeable from their shrill notes, produced by a stridulating drum on the abdomen. *C. orni* of the Old World fig. 526) punctures ash trees, causing the flow of manna. The CERCOPIDÆ contains the spittle bug (*Aprophora* *) which causes drops of foam on grass. The leaf hoppers,

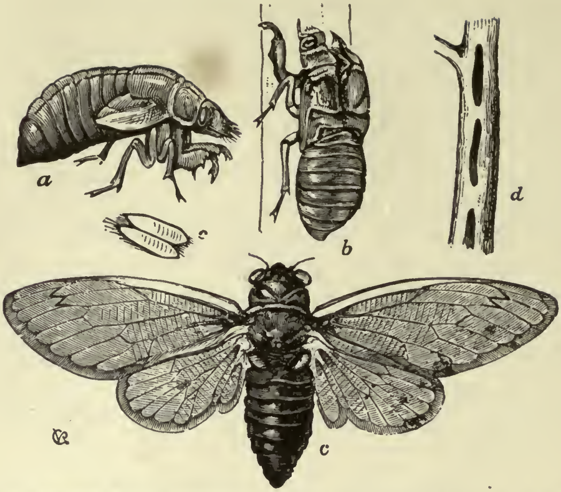


Fig. 525.—*Cicada septendecim*,* seventeen-year locust. (From Riley.) *a*, pupa; *b*, pupa case from which the imago, *c*, has escaped; *d*, twig bored for oviposition.

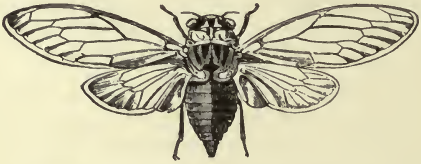


Fig. 526.—*Cicada orni.* (From Schmarda.)

or JASSIDÆ, contain some injurious forms, *Erythronura vitis** damaging the grape, while the true hoppers, MEMBRACIDÆ (fig. 527), are scarcely less injurious. None of these, however, are such serious pests as the plant lice and scale insects. In the COCCIDÆ, or scale insects, the wingless female dies after laying the eggs and covers them with her dead scale-like body. Here belong the cochineal insects, *Coccus cacti*,* the dried bodies of which furnish the pigment carmine, and the lac insects, *Coccus lacca*, as well as a host of injurious forms, like the orange scale, *Aspidotus aurantii*,* and the worse San José scale, *A. perniciosus*,* which has recently been spread throughout the country. The APHIDÆ, or plant lice, are soft-skinned and with their honey-containing excrement form a substratum for the growth of injurious fungi. They reproduce largely by parthenogenesis, a reason for their rapid multiplication; but their spread is not rapid, since the usually vivip-

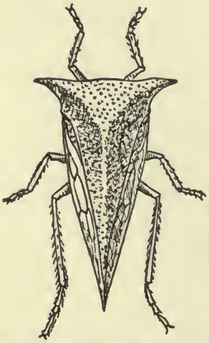


Fig. 527.—*Ceresa bubalus*,* buffalo leaf hopper. (After Marlatt.)

arous females are wingless. At times winged females appear and spread the pests. Winged males appear in the autumn, and the fertilized eggs endure the winter. Of all the species none is more injurious than the *Phylloxera vastatrix** of the grape, which with us does slight damage, but in Europe has destroyed whole vineyards. This is one of our returns for the many pests the Old World has sent us.

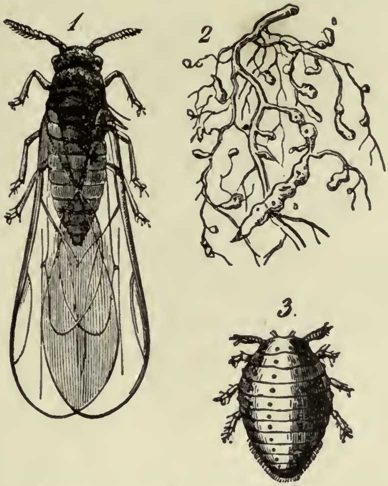


FIG. 528.—*Phylloxera vastatrix.* (From Ludwig-Leunis.) *1*, winged generation; *2*, grape root, with nodosities (*a*) caused by Phylloxera; *3*, wingless root-generation.

Sub Order III. APTERA. Wingless bugs with direct development, commonly known as lice, of which three species attack man, one living in the hair (*Pediculus capitis**), the others (*P. vestimentorum** and *Phthirius inguinalis**) upon the body. Other species live on other mammals.

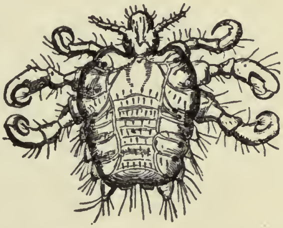


FIG. 529.—*Phthirius inguinalis*, crab louse. (After Leuckart.)

Order IX. Diptera.

Like the Rhynchota, the Diptera, or flies, are sucking insects, but the sucking tube or haustellum is different, here consisting of a tube formed of both labium and labrum, and containing stylets which include, besides mandibles and maxillæ (often rudimentary), the hypopharynx (fig. 488), the maxillary palpi being present. Only the anterior wings (hence Diptera) are well developed, the hinder wings being replaced by the halteres or balancers, small drumstick-like structures richly supplied with nerves and functioning as organs of equilibration. The thorax is, as in

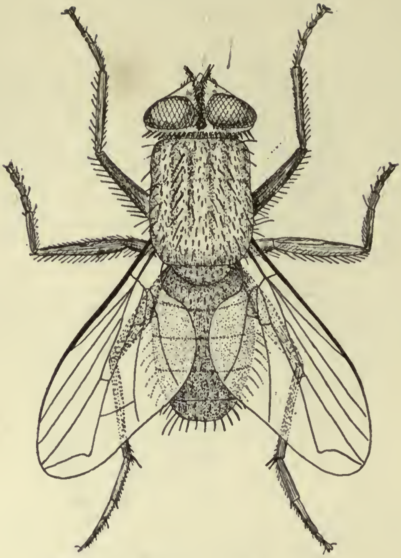


FIG. 530.—*Musca*, house fly (orig.).

the Hymenoptera, sharply marked off from head and abdomen, its somites being frequently fused. The development is holometabolous, two kinds of larvæ and pupæ occurring in its course. The larvæ are always apodal, but have either a distinct head with biting mouth parts or they are headless and have a rudimentary sucking apparatus (fig. 531). The pupæ are correspondingly either free with powers of motion, or are pupæ coarctatæ (p. 474). Development thus affords characters of systematic importance, and these are supplemented by differences in length of legs, antennæ, haustellum, and in body form. In number of species the Diptera stand next to the Coleoptera; in number of individuals they far exceed them.

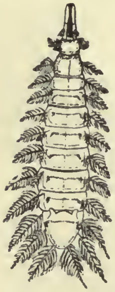


FIG. 531.—Larva of *Anthomyia canicularis*. (After Leuckart.)

Sub Order I. NEMOCERA. Elongate with long, many-jointed antennæ, long proboscis, long legs. The larvæ live in damp places or in water, where, lacking legs, they swim by movements of the body. The pupæ can also swim well. Best known are the innocuous crane flies (TIPULIDÆ) and the mosquitos (CULICIDÆ) with their numerous species affecting man, among them the forms which carry yellow fever, and *Anopheles*,* which distribute malaria. The CECIDOMYIDÆ include the injurious Hessian fly, *Cecidomyia destructor*,* and the pædogenetic *Miastor* (fig. 498).

Sub Order II. TANYSTOMA. Resemble the Muscariæ (with which they were formerly united) in the short stout bodies, short antennæ and legs. They are distinguished from them and resemble the Nemocera in their long proboscis and in development. The larvæ and pupæ live in damp places or in water and move rapidly, the larvæ having biting mouth parts. Here belong the black flies, SIMULIIDÆ, which excel the mosquitos in their viciousness, and the horse flies, TABANIDÆ, the females of which attack cattle and men, as well as horses, with their painful bites.

Sub Order III. MUSCARIÆ (Brachycera, after removal of Tanystoma). Body short, stout; antennæ three-jointed with a bristle (arista) (fig. 532); legs short, ending in an adhesive organ (pulvillus); larvæ headless living in decaying substances or parasitic in other animals. The MUSCIDÆ include the house flies (*Musca domestica* * and other species), the blow fly (*Calliphora vomitoria* *), and the flesh fly (*Sarcophaga carnaria* *), which is viviparous. The ASILIDÆ, or robber flies, prey on other insects, as do some of the SYRPHIDÆ: *Eristalis* * of this family has an aquatic 'rat-tailed larva,' one end being drawn out into a long breathing tube. ŒSTRIDÆ, bot flies; the larvæ always parasitic; those of the sheep bot (*Œstrus ovis* *) in the frontal sinuses of the sheep, causing the disease called 'staggers'; those of the ox warble (*Hypoderma lineata* *) just beneath the skin of cattle; those of the horse (*Gastrophilus equi*,* fig. 533) in the stomach of the horse. In the tropics *Dermatobia noxialis* lives as a larva in the human skin.

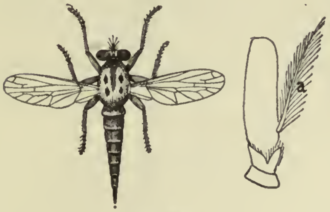


FIG. 532.

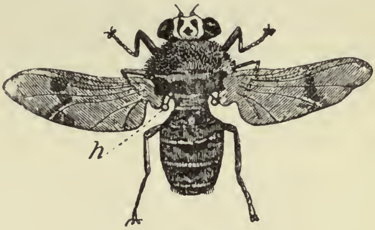


FIG. 533.

FIG. 532.—Left, *Erax bastardi*, robber fly; right, antenna of Muscid showing arista at *a*.
FIG. 533.—*Gastrophilus equi*,* bot fly. (From Hajek.) *h*, halteres.

Sub Order IV. PUPIPARA. Very active, often wingless forms living as parasites on mammals and insects; larval development inside the mother; pupation occurring soon after birth. *Melophagus ovinus*,* sheep tick; *Braula cæca*,* bee louse.

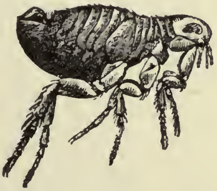


FIG. 534.—*Pulex irritans*,* flea. (From Blanchard.)

Order X. Aphaniptera (Siphonaptera).

In spite of the lack of wings the fleas are closely related to the Diptera, since they have doubtless descended from winged forms, as is shown by the fact that they have a holometabolous development. The larvæ, long and footless, live in decaying wood or dust in cracks in the floor, etc., and give rise to pupæ, both without traces of wings. Yet fleas and flies differ in that the fleas have similar body somites but the haustellum is lacking, the sucking tube being formed of labrum and mandibles, while the sharp maxillæ puncture the skin. Besides *Pulex irritans,** the flea that attacks man, many other species occur on other animals. In warm countries the jigger or chigoe, *Sarcophsylla penetrans,** attacks man, the female boring into the skin, usually under the nails, and there laying the eggs.

Order XI. Lepidoptera.

This group of butterflies and moths is the most sharply limited of any order of Hexapods. The wings, both pairs of which are well developed (rarely lacking, as in many female Psychidæ and some Geometridæ), are covered with scales (flattened hairs), and to these are due the frequently brilliant color patterns. Frequently the fore and hind wings are united by hooks (*frenulum*) on the latter, engaging in a *retinaculum* in the fore wing. The mesothorax is large and the smaller pro- and metathorax are closely united to it, giving the region a distinctness from head or abdomen. The mouth parts are peculiar (fig. 489), although foreshadowed in the Phryganids, and not fully developed in the Microlepidoptera. The mandibles are rudimentary or absent, while the fused maxillæ, greatly elongate, form the proboscis. Maxillary and labial palpi are present, the former smaller and often degenerate. The development is holometabolous; the larvæ, frequently called caterpillars (fig. 502), have biting mouth parts, the mandibles very strong; and also silk glands (sericteria), a pair of internal organs which open together on the labium and produce a secretion hardening to silk; besides the thoracic legs, prolegs, two to five pairs, are present. The pupæ are usually pupæ obtectæ, and are rarely free. In some the pupæ are ornamented with golden spots, whence the name chrysalides often applied to them.

Sub Order I. MICROLEPIDOPTERA. Small, inconspicuous; at rest holding the wings horizontally over the back; maxillary palpi very large; proboscis small. TINEIDÆ; the larvæ form a tube of the food material which they carry around with them. *Tinea pellionella,** the clothes moth. TORTRICIDÆ; the larvæ roll leaves into a tube. *Carpocapsa pomonella,** the codlin moth, the larvæ infesting apples.

Sub Order II. GEOMETRINA. Moths slender, the wings in pattern and shape recalling those of butterflies, but held horizontally when at rest; 'tongue' (proboscis) small; larvæ with two, rarely three, prolegs, known as span or measuring worms from their gait. Species numerous. Canker worms (*Paleacrita vernata,** *Alosophila pometaria,** females wingless), *Diastictis ribearia,** currant worm.

Sub Order III. NOCTUINA. Owlet moths; with short bodies; fore wings usually gray and ornamented by two spots and zigzag lines which at rest cover the frequently (as in *Catocala**) brightly colored hind wings. 1800 species in United States. *Hypena humuli*,* hop worm; *Aletia argillacea*,* cotton worm; *Leucania unipunctata*,* army worm; cut worms.

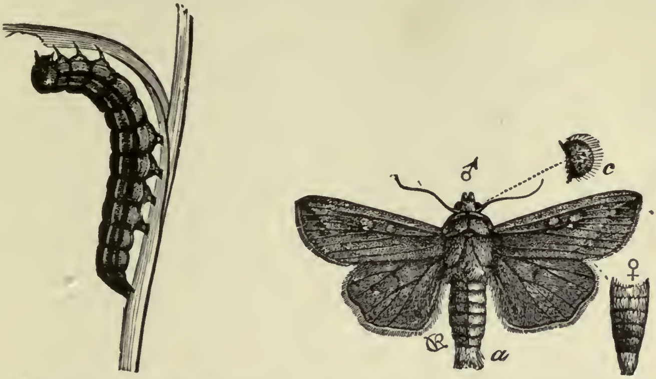


FIG. 535.—*Leucania unipunctata*, army-worm and moth. (From Riley.)

Sub Order IV. BOMBYCINA, silk worms. Body large, wooly, usually broad dull-colored wings; occasionally lacking in the females; proboscis frequently rudimentary. Antennæ long, pectinate; larvæ hairy, with well-developed spinning powers. Most important are the true silk worms (*Bombyx mori**), natives of China, while others, like *Telea polyphemus*,* furnish silk of value. Still others cause great damage to forest trees, among them the tent caterpillars (*Clisiocampa**) and the imported gipsy moth *Ocneria dispar* (fig. 72).

Sub Order V. SPHINGINA. Body long, stout; fore wings long, slender, hind wings shorter; proboscis very long; antennæ short; larvæ with a caudal spine. *Phlegethontius celeus*,* tomato worm; *P. carolina*,* tobacco worm. Considerably different are the SESIIDÆ, or 'clear wings,' which resemble bees and wasps.

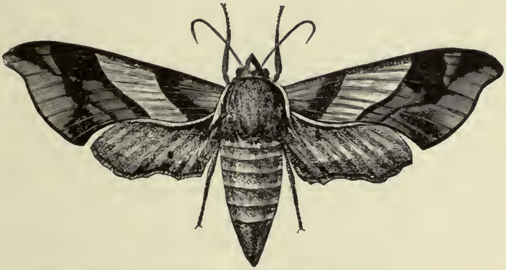


FIG. 536.—*Everyx myron*. (From Riley.)

Sub Order VI. RHOPALOCERA, butterflies. Body slender; wings held vertically when at rest, proboscis long; antennæ clubbed at the tip;

larvæ usually spiny; pupæ hung by a thread, never a cocoon. Species numerous. *Vanessa antiopa* * lives over winter; the species of *Pieris* * attack cabbages, etc.; *Papilio*,* swallow tails.

Class V. Diplopoda (Chilognatha).

The Diplopoda are usually united with the Chilopoda in a group of Myriapoda; but while they agree in having a head followed by numerous foot-bearing segments, they differ so greatly that no union is possible. The body is nearly cylindrical, although in the Polydesmids by lateral growth it may be flattened above; the legs are close together on the ventral surface, with the tracheal openings near them, while on the sides of the body are other openings of defensive glands, the foramina repugnatoria.

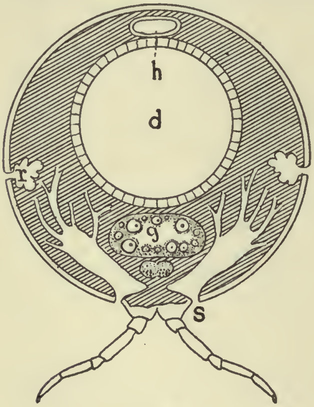


FIG. 537.

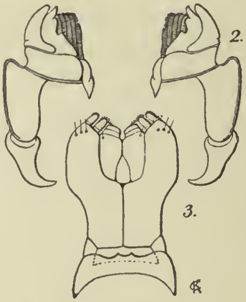


FIG. 538.

FIG. 537.—Schematic section of Diplopod (compare with fig. 481). *d*, digestive tract; *g*, gonad; *h*, heart; *r*, repugnatorial gland; *s*, spiracle and tracheæ.
FIG. 538.—Mouth parts of *Iulus*. (After Latzel.) *2*, mandibles of *I. molybdinus*; *3*, gnathochilarium (fused maxillæ) of *I. luridus*.

A more marked feature is that each segment of the body except the first four or five bears two pairs of appendages, which, with a similar duplicity in chambers of the heart, tracheæ, ganglia, etc., shows that a fusion has occurred. The anterior somites bear at most but a single pair of legs; both legs and antennæ are short. The head bears, besides the antennæ, but two pairs of appendages, a pair of several-jointed mandibles (fig. 538), and a pair of rudimentary maxillæ fused to a single plate, the gnathochilarium.

The gonads lie ventral to the intestine far back in the body, those of the right and left sides enclosed in a single sac; the ducts open separately on the second somite of the trunk. The spermatozoa are not motile. The legs of the seventh segment of the male are used in copulation. The young escape from the egg with three pairs of legs, a point once thought to show resemblances to the Hexapoda, but which does not, for these legs are on the fourth, sixth, and seventh somites of the body. The IULIDÆ have elongate cylindrical bodies; *Spirobolus.** GLOMERIDÆ short, capable of rolling into a ball; POLYDESMIDÆ, with wing-like processes to the segments, giving them a flattened appearance. PAUROPODA: minute; body with twelve segments, tending to fuse to six. *Pauropus,** *Eurypauropus.** More uncertain in position are the SYMPHYLA (*Scolopendrella* *), but from the position of the genital opening they are placed here.

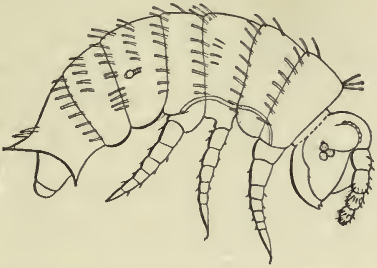


FIG. 539.—Hexapod young of *Strongylosoma.* (After Metschnikoff.)

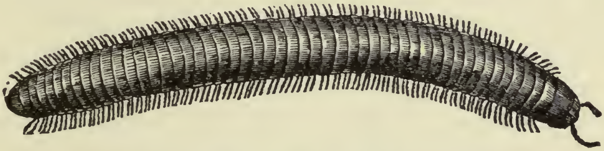


FIG. 540.—*Iulus maximus.* (After Schmarda.)

Summary of Important Facts.

1. The ARTHROPODA are animals with evident internal and external segmentation (metamerism).

2. The metamerism is expressed internally in the ladder-like nervous system, in the structure of the heart, and in the arrangement of segmental organs and tracheæ so far as these are present.

3. The outer segmentation is expressed in the rings of the chitinous coat of the body as well as in the metameric arrangement of the appendages.

4. From the similarly metameric Annelida the Arthropoda are distinguished by the presence of jointed appendages, at most a pair to a somite. The appendages may be divided according to function into antennæ, jaws, accessory jaws, feet, and swimmerets.

5. A further distinction is the grouping of the somites into regions of which usually head, thorax, and abdomen are recognized.

6. The head bears the tactile and eating appendages; the

thorax those used in locomotion (pereiopoda), the abdomen the swimmerets (pleopoda), or it lacks appendages.

7. By fusion of head and thorax a cephalothorax is produced; a postabdomen may be separated from the abdomen.

8. The eyes are either ocelli or compound eyes.

9. Hermaphroditism is rare; reproduction is by eggs; frequently there is parthenogenesis, rarely pædogenesis. The eggs usually have a superficial segmentation.

10. The Arthropoda are divided into Crustacea, Acerata, Malacopoda, Insecta, and Diplopoda.

11. The CRUSTACEA respire by gills; they usually have two pairs of antennæ, and usually biramous feet; the reproductive ducts open near the middle of the body.

12. The Crustacea are divided into Trilobitæ, Phyllopoda, Copepoda, Ostracoda, Cirripedia, and Malacostraca.

13. Phyllopoda, Copepoda, Ostracoda, and Cirripedia are frequently called Entomostraca; they have a shell gland and the nauplius as a larval stage.

14. The *Trilobitæ* are extinct forms with one pair of antennæ, and the body divided by longitudinal grooves into three regions.

15. The *Phyllopoda* have variable segments and primitive leaf-like feet recalling the parapodia of the annelids.

16. The *Copepoda* are without shells and have biramous feet.

17. The *Ostracoda* have reduced bodies enclosed in a bivalve shell.

18. The *Cirripedia* are usually hermaphroditic and are sessile.

19. The *Malacostraca* have 20 (21) segments, of which 7 (8) are abdominal; the male sexual openings are on the 13th, the female on the 11th, segment; the excretory organ is the antennal gland; the larva is a zoea, rarely a nauplius.

20. The Malacostraca are divided into Leptostraca, Thoracostraca, and Arthrostraca.

21. The *Leptostraca* have twenty-one somites; they are closely related to the Phyllopoda.

22. The *Thoracostraca* or *Podophthalmia* (Schizopoda, Stomatopoda, Decapoda) have stalked eyes and some or all of the thoracic somites fused with the head to a cephalothorax.

23. The *Arthrostraca* or *Edriophthalmia* have sessile eyes and have seven free thoracic segments. They are divided into Amphipoda and Isopoda.

24. The ACERATA lack antennæ; the body is divided into cephalothorax and abdomen; the cephalothorax bears six pairs of

appendages; the genital ducts open on the seventh somite; the respiratory organs—gills, lungs, or trachea—develop from the abdominal appendages.

25. The Acerata are divided into Gigantostraca and Arachnida.

26. The *Gigantostraca* are large, and breathe by gills. The only living forms are Xiphosures.

27. The *Arachnida* breathe by lungs or by tracheæ derived from lungs, the openings to which are on the abdomen; they have a pair of cheliceræ, a pair of pedipalpi, and four pairs of legs; they have in addition several pairs of highly developed ocelli.

28. The Arachnida are divided into nine orders: Scorpionida, Phrynoidea, Microthelyphonida, Solpugida, Pseudoscorpii: Phalangida, Araneina, Acarina, and Linguatulida.

29. The *Scorpionida* have chelate pedipalpi and a postabdomen terminated by a sting.

30. The *Phrynoidea* have the first pair of legs tactile and not used in walking, and a continuous cephalothorax.

31. The *Microthelyphonida* and the *Solpugida* have three 'thoracic' segments free. The Microthelyphonida have a long, jointed postabdomen, lacking in the Solpugida.

32. The *Pseudoscorpii* resemble the Scorpionida, but lack the postabdomen and sting.

33. The *Phalangida* have very long legs and spider-like bodies.

34. The *Araneina* have an unsegmented abdomen, bearing four or six spinnerets and numerous spinning glands. They are divided into Tetrapneumones, with four lungs, and Dipneumones, with two lungs and two tracheæ.

35. The *Acarina* have cephalothorax and abdomen fused and the mouth parts for sucking. Several species are parasitic on man.

36. The *Linguatulida* are complete parasites, ribbon-like and without legs; the young live in the lungs and liver.

37. The *Tardigrada* and *Pycnogonida* agree with the Arachnida in the number of walking legs. Their position is very uncertain.

38. The MALACOPODA are intermediate between Annelida and Insecta. They have indistinctly segmented bodies with parapodia-like feet, segmental organs, and tracheæ.

39. The INSECTA breathe by tracheæ; the head bears four pairs of appendages: antennæ, mandibles, maxillæ, labium; since tracheæ are present the circulatory system is reduced; the reproductive organs open at the hind end of the body.

40. The Insecta are divided into Chilopoda and Hexapoda.

41. The *Chilopoda* have numerous body segments with a pair

of long legs on each; close behind the head are a pair of poison feet.

42. The *Hexapoda* have the body divided into head, thorax, and abdomen.

43. The abdomen consists of a varying number of somites and lacks appendages.

44. The thorax consists of three segments, pro-, meso-, and metathorax, each bearing a pair of legs, and meso- and metathorax usually a pair of wings each.

45. The head bears, besides three pairs of mouth parts, an unpaired upper lip (labrum) and two compound eyes, besides usually one to three ocelli.

46. The structure of the mouth parts varies with the food; they are either biting, licking and sucking, or piercing in function.

47. Wingless insects usually have a direct (ametabolous) development with numerous ecdyses.

48. Winged insects (and many without wings which have descended from winged forms) have a metamorphosis in which the larva differs more or less from the imago (metabolous insects); the larva never has wings.

49. An incomplete metamorphosis (hemimetabolous development) occurs when the larva with each molt becomes more like the adult, developing wing pads which with each ecdysis become larger.

50. In complete metamorphosis (holometabolous development) the changes occur in the last molting stage, which is a stage of rest, the pupa.

51. Classification of Hexapoda is based upon structure of mouth parts and wings as well as upon regional relations and development.

52. The *Apterygota* are wingless, ametabolous Hexapoda with biting mouth parts.

53. The *Archiptera* have biting mouth parts with incompletely fused labium, net-veined wings, and incomplete metamorphosis.

54. The *Orthoptera* resemble the Archiptera in mouth parts and development, but have parchment-like wings.

55. The *Neuroptera* have net-veined wings and a holometabolous development; the mouth parts are modified.

56. The *Coleoptera* are biting insects with the fore wings changed to elytra; they differ from the somewhat similar Orthoptera by the complete metamorphosis.

57. The *Strepsiptera* are parasitic forms allied to the Coleoptera.

58. The *Hymenoptera* have partly biting, partly licking mouth

parts; membranous wings with few nervures and holometabolous development.

59. The *Rhynchota* are hemimetabolous or ametabolous, with piercing mouth parts; the bed bugs and the Pediculina are parasitic.

60. The *Diptera* are holometabolous, with piercing mouth parts and not more than one pair of wings. The larvæ of the Œstridæ are parasitic.

61. The *Aphaniptera* are holometabolous, wingless, parasitic, with sucking mouth parts.

62. The *Lepidoptera* have the wings covered with scales; labium and labrum rudimentary, the maxillæ altered to a sucking tube; the development holometabolous.

63. The DIPLOPODA have a head with three pairs of appendages; the trunk with double segments, each bearing two pairs of legs, the genital openings anterior.

64. The term Myriapoda is frequently used to include Chilopoda and Diplopoda.

PHYLUM VIII. CHORDATA.

Within recent years it has been realized that a number of animals, formerly distributed among various groups, possess structural features of great importance which ally them to the vertebrates. On the other hand they lack the vertebræ and many other features characteristic of that group, so that the name cannot be extended to include them. Yet since all these forms possess, as a temporary or a permanent feature, a structure known as the chorda dorsalis or notochord, the term Chordata has been adopted to include them.

The notchord is a smooth elastic rod arising, in development, from the entoderm and coming to lie between the digestive tract and the nervous system (fig. 9). In all Chordates the anterior (pharyngeal) portion of the alimentary canal develops one or more pairs of pockets which grow outwards and fuse with the ectoderm. The fused portion then breaks through, and the pockets become converted into gill slits (branchial clefts), which, in the lower forms, allow the passage of water over the gills which line the slits.

The central nervous system lies on one side of the alimentary canal, there being no ring of nervous matter (Enteropneusta excepted) around the œsophagus, such as is so common in the invertebrata. It arises as a medullary plate on the dorsal side of the body around the blastopore. The edges of this plate are rolled inwards, converting the plate into a tube with nervous walls and a central canal. From this, as will readily be seen, it happens, when the blastopore remains open behind (fig. 547, *ne*), that a temporary communication, the neurenteric canal, exists between the neural and alimentary canals.

On the other hand the chordates share with the annelids and arthropods a segmentation of the body which, however, is internal and only exceptionally is visible from the surface.

The Chordates include the Leptocardii, the Tunicata, doubtfully a group of Enteropneusta, and the Vertebrata.

Sub Phylum I. Leptocardii (Cephalochordia, Acrania).

Until recently but a single genus (*Amphioxus*) was recognized as belonging to this group, and this form, known for over a hundred years, was at first described as a mollusc (*Limax lanceolatus*). Its chordate nature was first recognized by Johannes Müller, while the embryological researches of Kowalewsky showed its close relations to the Tunicata.

In structure it is comparatively simple. The fish-like body, pointed at either end (whence *Amphioxus*), lacks paired appendages, but has a median fold or fin best developed at the caudal end. The epithelium covering the body is but a single cell in thickness and allows the underlying muscle segments to show through. It differs from the fishes in lack of skull (Acrania), vertebræ, brain, heart, and kidneys, although the rudiments of brain and excretory organs are present. Connective tissue is almost entirely absent, the body consisting of much-folded epithelia separated by thin gelatinous layers.

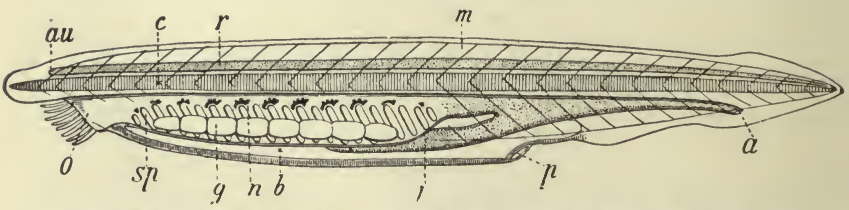


FIG. 541.—*Amphioxus lanceolatus.* (Diagram after Boveri.) *a*, anus; *au*, eye; *b*, peribranchial space; *c*, notochord; *g*, gonads; *l*, liver; *m*, muscles; *n*, nephridia; *o*, mouth; *p*, atrial opening; *r*, spinal cord; *sp*, gill slits.

An axial skeleton is present in the notochord, which extends the whole length of the body (fig. 541, *c*). Above it lies the spinal cord, with a central canal, which expands in front into a rudimentary cerebral vesicle. A pigment spot in this brain is the primitive eye, but other places are sensitive to light. The olfactory organ is an unpaired pit on the anterior end of the body; and at its bottom, in the young, is an opening, the anterior neuropore, which leads into the anterior end of the neural canal. It is a point of delayed closure of the embryonic medullary folds.

Of the alimentary tract more than a third is occupied by the pharynx with the gill slits. It begins with an oval mouth, surrounded by cirri, and is perforated by numerous gill slits, between which elastic gill arches form a support for the walls (fig. 542, *kb*). In the young the gill slits open directly to the anterior, but later, somewhat as in Tunicata, into a peribranchial chamber (*b*) which allows the escape of the water through a porus branchialis (fig. 541, *p*), behind the middle of the body. On the ventral floor of the pharynx is a ciliated hypobranchial groove (fig. 542, *e*), the homologue of the tunicate endostyle and of part of the vertebrate thyroid. It leads back to the straight digestive tract which opens on the left side near the end of the body, and bears in front a blind liver sac which extends forward into the gill region (figs.

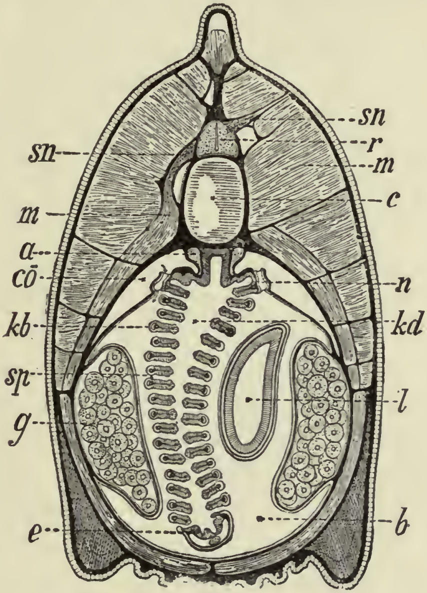


FIG. 542.—Section of the gill region of *Amphioxus*. (After Lankester and Boveri.) *a*, aorta descendens; *b*, peribranchial space; *c*, notochord; *cö*, cœlom (branchial body cavity); *e*, hypobranchial groove, beneath it the aorta ascendens; *g*, gonad; *kb*, gill arches; *kd*, pharynx; *l*, liver; *m*, muscles; *n*, nephridia, on the left with an arrow; *r*, spinal cord; *sn*, spinal nerve; *sp*, gill slit.

541, 542, *l*). The vascular system, with colorless blood, consists of a dorsal arterial (*a*) and a ventral venous trunk connected by lateral loops or arches. The ventral trunk begins as a subintestinal vein under the intestine, branches as a portal vein over the liver, and, reuniting again in a ventral vessel, continues forward, as the aorta ascendens, below the gills. From this the vascular arches—gill arteries—pass up between the gill slits and form the dorsal vessel, the aorta descendens. A true heart is lacking, but various parts of the vessels—a part of the ventral trunk and the bases of the gill arteries—are contractile, whence the name Leptocardii.

As the pharynx lies in the peribranchial chamber, the digestive portion of the tract lies in a true body cavity or cœlom, which extends forward (fig. 542, *cö*) into the branchial region as well as into the gill-walls (branchial cœlom) and into the outer walls of the peribranchial chamber (peribranchial cœlom). In the peribranchial cœlom are the gonads (*g*), a series of pouch-like cell follicles which, by dehiscence, allow their products to escape into the peribranchial chamber. Into this chamber also empty the excretory organs which were long sought for in vain. These are (*n*) a series, on right and left sides, of ciliated canals apparently corresponding to the pronephros of the vertebrates. Each canal begins with at least one ciliated nephrostome in the cœlom and opens separately like an annelid nephridium.

Like the structure, the development is comparatively simple. The following points deserve special mention: (1) The eggs have a nearly equal segmentation (fig. 96). (2) A typical invaginate gastrula (fig. 105) occurs. (3) The mesoderm arises as a series of pouches, right and left, from the mesenteron, which later separate and represent the primitive segments. Hence these are clearly mesothelial in nature. From the cavities of these arises the body cavity, which is consequently an enterocœle. (4) The dorsal surface of the entoderm between these cœlomic pouches becomes folded off from the rest and forms the notochord, which lies between the digestive tract and the nervous system. (5) The nervous system arises from a longitudinal groove which becomes folded into a tube and is connected for a while with the digestive tract by a neurenteric canal.

*Amphioxus** contains a few closely related species which occur on our southeastern coast, in Europe, Indian Ocean. Recently other genera have been described—*Asymmetron** in America, *Heteropleuron* in the South Seas. The animals live in quiet bays and bury themselves in the sand, with only the mouth above the surface. Like all animals with rudimentary eyes, they shun the light and are greatly excited by strong illumination.

SUB PHYLUM II. TUNICATA (UROCHORDA).

In their adult condition the Tunicata, or sea-squirts, bear some resemblance to the siphonate mollusca, especially in the possession of incurrent and excurrent orifices, usually close together, and a mantle. Hence these forms were long associated with the molluscs; later they were associated with the worms, but their development shows them to be more nearly related to the vertebrates.

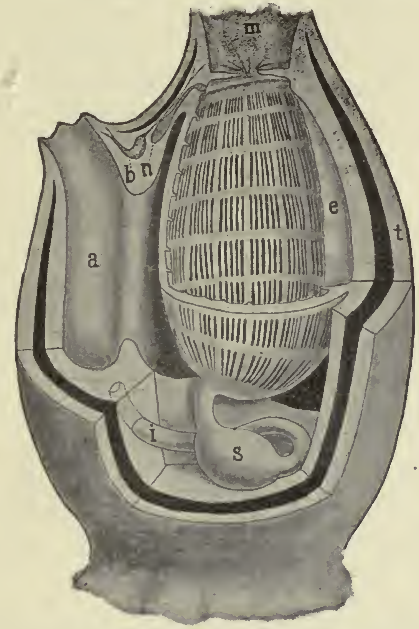


FIG. 543.—Diagram of a tunicate (orig.). *a*, atrium; *b*, nervous ganglion; *e*, endostyle; *i*, intestine; *m*, mouth; *n*, subneural gland; *s*, stomach; *t*, tunic. In the centre the branchial basket with the gill slits communicating with the peribranchial space, and this in turn with the atrium.

The group owes its name to the tunic or mantle—lacking in the Copelatæ—an envelope (fig. 543, *t*) which is formed like a cuticle by the epithelium of the skin, but which is distinguished from ordinary cuticula by its structure. It much resembles connective tissue in that cells from the mesoderm wander into the ground substance, which is sometimes fibrous, sometimes homogeneous, and has an interesting chemical nature. It consists of the same proportions of carbon, oxygen, and hydrogen ($C_6H_{10}O_5$) as cellulose and agrees with this substance, so characteristic of plants, in its reactions (blue color with iodine-iodide of potassium and sulphuric acid, violet with chloriodide of zinc). Nowhere else among animals is there such a rich formation of cellulose.

The anterior part of the digestive tract is modified into a pharynx or branchial chamber, the walls of which become perforated with a varying number of gill slits, these leading either directly to the exterior or, more usually, into a peribranchial chamber, and from this to a cloaca or atrium (*a*), before reaching the outside world. While the respiratory water passes through the gill slits the food particles which it contains are received by a ring-shaped ciliated band (peripharyngeal band) and, enveloped by mucus, are led to the œsophagus. This mucus is formed by a ciliated glandular groove, the endostyle (*e*), on the ventral surface of the pharynx.

Between the gill region (end of the endostyle) and the stomach lies the ventral heart enclosed in a pericardium. It has the peculiarity, met nowhere else, of changing the direction of its contractions at frequent intervals; after the heart has driven the blood for a time to the gills it rests a while and then begins to force the blood in the opposite direction, pumping it from the gills and sending it towards the stomach.

If we add to the foregoing that a dorsal ganglion and a hermaphroditic gonad are present, the striking features of the group are enumerated. The extreme forms, the Copelatæ and the Thaliacea, are rather remote, but they are connected by intermediate forms, the Ascidiæ and Pyrosomas.

Order I. Copelatæ.

These small forms—one or a few centimeters in length—are pelagic; they have the anterior end inserted in a gelatinous envelope or ‘house’ which replaces the lacking tunic. They swim like a tadpole by means of a tail which arises from the hinder end of the trunk. The alimentary canal (fig. 544) is bent on itself, and both it and the two large gill slits, in contrast to all other tunicates, open directly to the exterior. The heart (lacking only in the Kowalewskidæ) is ventral and the hermaphroditic gonads and the nervous system dorsal. The latter consists of a cerebral ganglion, with beside it an extremely simple auditory organ and a ciliated groove, and farther a chain of ganglia extending into the tail. The notochord, a gelatinous structure enclosed by a sheath of cells, forms the skeletal axis of the tail ventral to the nerve cord and gives attachment to muscles. *Oikopleura,* Appendicularia,* Fritillaria; Kowalewskia.*

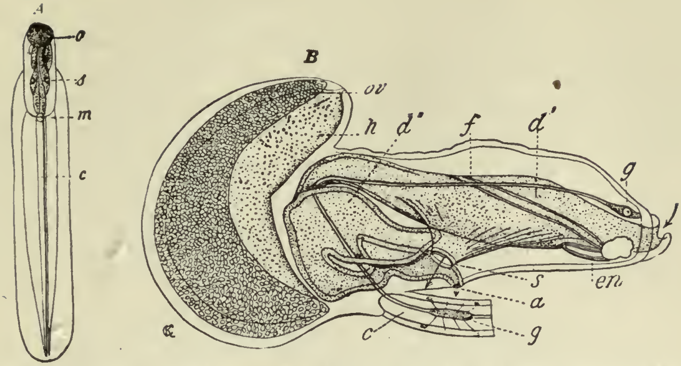


FIG. 544.—*Oikopleura cophocerca.* (After Fol.). *A*, the whole animal, removed from its 'house,' dorsal view; *B*, body, side view with base of tail. *a*, anus; *c*, notochord; *a′*, branchial region; *d″*, stomach; *en*, endostyle; *f*, ciliated peripharyngeal bands; *g*, *g′*, brain and first ganglion of tail; *h*, testis; *m*, mouth; *o*, *ov*, ovary; *s*, gill slits.

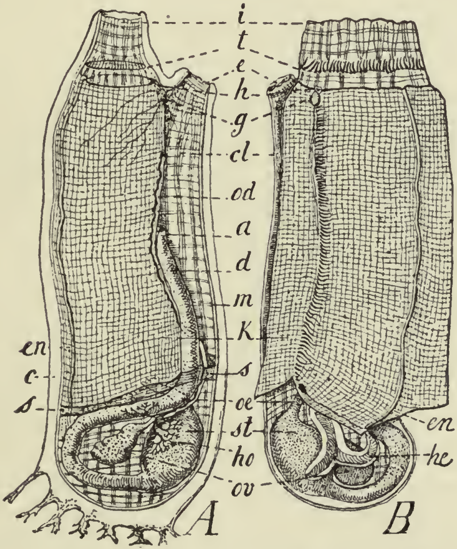


FIG. 545.—*Ciona intestinalis.* *A*, from the left side, the cellulose tunic and dermal muscular sac removed; *B*, from the right side, the tunic entirely removed, pharynx opened from the mouth. *a*, anus; *c*, cellulose tunic below with adhesive processes; *cl*, cloaca; *d*, rectum; *e*, atrial opening; *en*, endostyle ending above in the peripharyngeal band; *g*, ganglion; *h*, mouth of the 'hypophysis'; *hr*, heart, with pericardium; *ho*, branched testes; *i*. oral opening; *k*, gill sac; *m*, muscular sac; *oe*, œsophagus; *od*, oviduct, the black line beside it the vas deferens; *ov*, ovary; *s*, partition between atrium and body cavity; *st*, stomach; *t*, crown of tentacles.

Order II. Tethyoidea (Ascidiæformes).

With the exception of the pelagic Pyrosomidæ all of the ascidians are attached to rocks, etc., in the sea. The greater necessity for protection caused by this sedentary life has resulted in a great development of the cellulose tunic, which, enveloping the internal organs, gives these animals a swollen, somewhat shapeless appearance. Two openings, mouth and atrial opening, lead into the interior, and the water which issues from these, when the animals are taken from the ocean, has given them the common name of 'sea-squirts.'

On removing the tunic, which is but slightly attached to the other parts except at mouth and atrial opening, a muscular sac is seen (fig. 545), the fibres running circularly and longitudinally. Inside this sac are the viscera, the pharyngeal region by far the most conspicuous. The mouth leads to a short tube with tentacles (*t*), and then to the pharynx, a wide sac which lies in a large cavity, the peribranchial chamber, the walls of the pharynx and the enclosing space uniting on the ventral side (fig. 543). The pharyngeal walls are perforated like a net by small ciliated gill slits, arranged in longitudinal and transverse rows (fig. 546), through which the water received from the mouth passes into the peribranchial chamber and thence to the atrium, and so out to the external world.

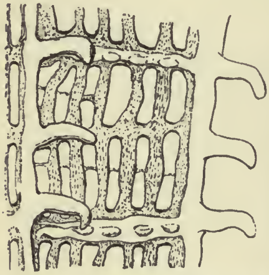


FIG. 546.—*Ciona intestinalis*, a bit of the wall of the gill sac enlarged to show the gill slits.

While the respiratory water thus passes out in a nearly direct course, the food particles which it contains pass into the digestive tract. By means of a ciliated tract (peripharyngeal band) just inside of the tentacles and surrounded by mucus secreted by the endostyle (or hypobranchial groove), the food is carried back to the œsophagus (*oe*) at the base of the gill chamber, and thence to the stomach (usually provided with liver glands), and on to the intestine. The anus is at the base of the special portion of the peribranchial chamber, which also receives the genital ducts and hence is known as the cloaca or atrium.

In the body cavity, which is greatly reduced in the species with concentrated bodies, occur the digestive tract, the sexual organs, and the heart; the latter, frequently S-shaped, extends between the stomach and the endostyle. Opposite to the endostyle is the ganglion in the dorsal wall between oral and atrial openings. Below it (rarely above it) is a branched subneural gland which, from its relations and its opening into the prebranchial part of the alimentary tract, has been compared to the vertebrate hypophysis. In many there exist special excretory organs, numerous blind vesicles filled with excreta.

From the eggs are hatched small swimming tadpole-like larvæ (fig. 547), resembling *Appendicularia* and, like it, consisting of trunk and tail, in which the chordate features are strongly marked. The digestive tract is confined to the trunk; dorsal to it lies the tubular nervous system in which three parts are recognizable: in front a vesicular brain with a simple eye and an otocyst imbedded in its walls; farther back a narrower portion ('medulla oblongata'); lastly, a spinal cord extending into the tail. In the axis of the tail is a notochord which extends forward a short distance into the trunk between digestive tract and nervous system.

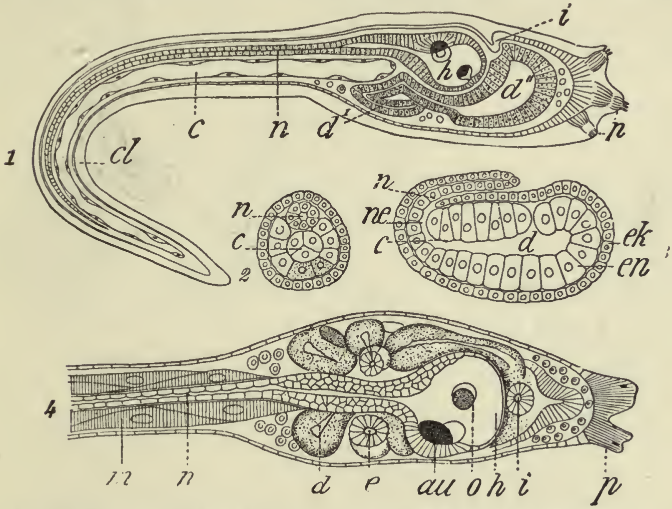


Fig. 547.—Development of an Ascidian. (After Kupffer and Kowalevsky.) *1*, larva, just hatched; *2*, cross-section through the tail of a slightly younger larva; *3*, much younger stage, formation of notochord and nervous system; *4*, anterior end of a larva just before attachment. (*2*, *Phallusia mentula*; *3*, *4*, *Ph. mammillata.*) *au*, eye; *c*, notochord; *cl*, tunic; *d*, digestive tract; *d'*, its nutritive, *d''*, its respiratory division; *e*, atrial vesicle; *ek*, ectoderm; *en*, entoderm; *h*, brain; *i*, oral invagination; *m*, muscles of tail; *n*, neural tube; *ne*, neurenteric canal; *o*, otocyst.

In the metamorphosis of the free larvæ into the sessile ascidians four processes are important: (1) The larvæ attach themselves by means of three ventral anterior papillæ; (2) The tail is retracted and, after preliminary fatty degeneration, is absorbed; (3) The body becomes more or less spherical by development of the tunic;

(4) Two dorsal invaginations are formed, these grow together, envelop the pharyngeal region, and form the atrium and peribranchial chamber. It is to be noted that this arises from the dorsal surface and extends ventrally, while the peribranchial chamber of *Amphioxus* arises by folds which grow ventrally over the pharynx.

Besides sexual reproduction many ascidians reproduce by budding. Where this occurs it results in the formation of colonies, a matter of systematic importance.

Sub Order I. MONASCIDIÆ. Simple ascidians of considerable size; sometimes with transparent, sometimes with thick opaque tunic. The CLAVELLINIDÆ produce small colonies by basal budding, each individual with its own test; *Perophora*.* CYNTHIIDÆ, test leathery, oral and atrial openings four-lobed; *Cynthia*.* MOLGULIDÆ, oral opening, six-lobed, atrial four-lobed. *Molgula*,* *Eugyra*.*

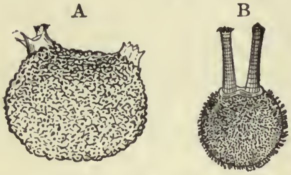


FIG. 548.

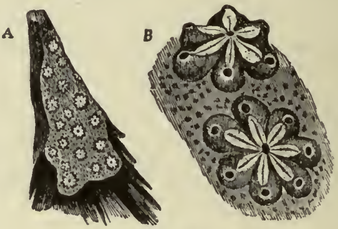


FIG. 549.

FIG. 548.—*A. Molgula manhattensis**; *B, Eugyra pillularis*.* (From Verrill.)
FIG. 549.—*Botryllus violaceus*. (After Carpenter.) *A*, small colony of eighteen individual groups; *B*, two individual groups somewhat enlarged.

Sub Order II. SYNASCIDIÆ. Compound ascidians consisting of numerous small individuals imbedded in a common cellulose tunic and forming considerable crusts on stones, plants, etc. Usually (fig. 549) the individuals of a colony are divided into small groups, the oral openings (6–20 in number) forming a rosette around a common central atrium. *Distaplia*,* *Leptoclinum*,* *Polyclinum*,* *Amaroucium*,* *Botryllus*.*

Sub Order III. LUCIÆ. Free-swimming pelagic synascidians, having the form of a hollow cylinder closed at one end. The animals imbedded in the tunic vertically to the axis of the cylinder, the oral apertures on the outside, the atrial in the central cavity. *Pyrosoma*, very phosphorescent, tropical, some species four feet long.

Order III. Thaliacea (Salpæformes).

These, like the Luciæ and Copelatæ, are pelagic, and play an important part in the plankton, either by the vast numbers of small individuals or by the formation of colonies of considerable size. In form a *Salpa* may be compared to a barrel formed outside of a cellulose tunic, lined internally with a muscular wall. The muscles run circularly (fig. 550), are six or eight, not always closed rings, like hoops. By their contraction the water is expelled through the posterior or atrial end of the body, while fresh water on their relaxation enters the other or oral aperture. By the reaction the animals swim through the water with the oral end in front. The cavity of the barrel corresponds to pharyngeal and peribranchial chambers of the ascidian. In the Dolioliidæ the two chambers are separated by a partition perforated by gill slits (fig. 551); in the common *Salpæ* the partition is reduced to a bar with transverse rows of cilia so that branchial and peribranchial chambers are not distinct; yet the endostyle and the peripharyngeal band are retained.

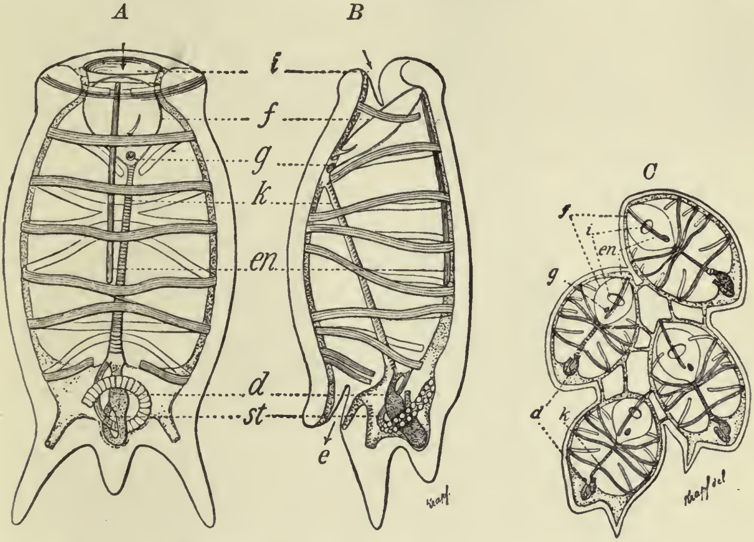


Fig. 550.—*A*, *B*, *Salpa democratica* with stolon, ventral and lateral views; *C*, *Salpa mucronata*, part of a young chain not yet separated. *a*, anus; *c*, tunic; *d*, digestive tract; *e*, atrial opening; *en*, endostyle; *f*, peripharyngeal groove; *g*, ganglion with horseshoe-shaped eye, and near it the tentacle and hypophysial groove; *h*, testis; *i*, mouth; *k*, gill; *m*, muscle hoops; *st*, stolo prolifer.

The viscera lie in the muscular sac, where the branchial bar and the endostyle meet and are usually compacted into a mass, the ‘nucleus’ (intestine, liver, gonads, heart). The ganglion is distinct and lies dorsally opposite the endostyle, just in front of the branchial bar. Associated with it is a horseshoe-shaped eye.

For a long time two kinds of *Salpæ* have been known, one solitary, the other consisting of numerous individuals connected together like a chain or a rosette (fig. 550, *C*). At the beginning of the last century the poet Chamisso discovered that the chain salps were produced by the solitary individuals, and that these in turn came from the chain form, a peculiar type of reproduction to which Steenstrup later gave the name alternation of generations. The solitary salp is asexual; gonads are lacking, but near the hinder end is a budding cone or stolo prolifer from which one after another bud colonies of salps. When the first is separated a second matures and a third begins. These colonial forms, the chain salps, are sexual, and each produces a single egg from which a solitary individual is formed.

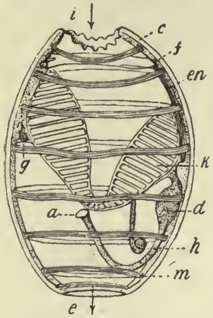


Fig. 551.—*Doliolum denticulatum.* (For explanation of letters see fig. 550.)

Since both the solitary and the chain forms have received names, the species of *Salpa** now have double names like *Salpa democratica-mucronata*, *democratica* being the asexual, *mucronata* the sexual, individual, etc. From the true *Salpæ Doliolum** is distinguished by the better developed gills, the complete muscular bands, and a more complicated alternation of generations.

SUB PHYLUM III. ENTEROPNEUSTA (HEMICHORDIA).

The few marine forms here included are decidedly worm-like, and, like many worms, they burrow in the mud. The body consists of three parts—proboscis, collar, and body (fig. 552). The proboscis contains a cavity opening to the exterior by a dorsal pore, while two similar cavities in the collar open separately. These can be filled with water, and by alternately enlarging and contracting these parts the animal is able to burrow like a razor clam (*Ensis*). The mouth lies ventral and in front of the collar and leads into a digestive tract, which in its anterior part is perforated by numerous paired gill slits, while the part behind it is covered with hepatic cæca. The intestine is supported in the cœlom by dorsal and ventral mesenteries, and is accompanied by a dorsal and a ventral blood-vessel, to which are added lateral canals and numerous anastomoses. A vesicle on the dorsal vessel in the proboscis is called the heart. The nervous system is very peculiar. There is a dorsal portion lying in the collar region, which is produced by inrolling, as is the central nervous system in the Chordates, and a ventral part, as yet lying in the ectoderm, the two being connected by nerves in the collar. The gonads are numerous follicles lying between gill and liver region and opening to the exterior.

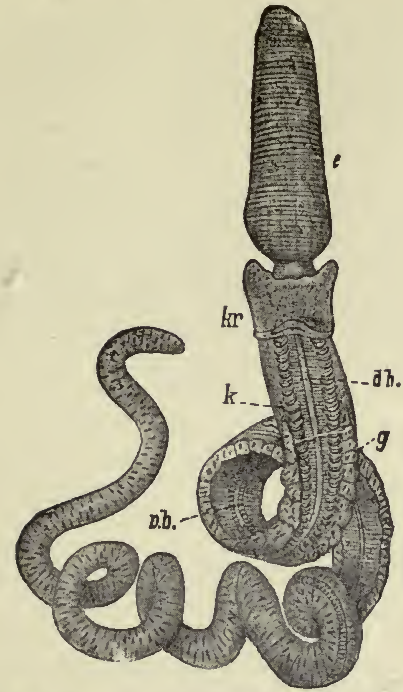


Fig. 552.—*Balanoglossus kowalewskii.** (From Korschelt-Heider, after A. Agassiz.) *db*, dorsal blood-vessel; *e*, proboscis; *g*, sexual region; *k*, gill region; *kr*, collar; *vb*, ventral blood-vessel.

The systematic position of the Enteropneusta is not settled beyond a doubt. In the possession of gill slits and in the formation of the dorsal nervous system it closely resembles the other chordates, and the resemblance is strengthened by similarities in details of structure of the gills. The advocates of this view recognize the notochord in a blind tube, surrounded by tough membrane and thickened beneath, which extends from the pharynx into the proboscis. Embryology throws but little light on the problem. Some species have a direct development (fig. 553, *B*, *C*), while others have a larva (Tornaria, fig. 553, *A*) which so resembles the larvæ of certain echinoderms that it was long held to belong to that phylum. The chief resemblances are in the relations of the ciliated bands to the alimentary tract and in the presence of the proboscis cavity,

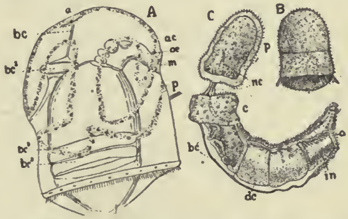


Fig. 553.—*A*, Tornaria larva of *Balanoglossus*. (After Morgan.) *a*, apical plate; *ac*, preoral part of ciliated band; bc^1, bc^2, bc^3, cœlomic pouches; *m*, mouth; *p*, postoral part of ciliated band *B*, *C*, two stages of *Balanoglossus* with direct development. (After Bateson.) *a*, anus; *bc*, branchial clefts; *c*, collar; *dc*, digestive part of alimentary canal; *in*, intestine; *nc*, 'notochord'; *p*, proboscis.

which, like the ambulacral system, opens to the exterior. Two deep-sea forms, *Cephalodiscus* and *Rhabdopleura*, have the same type of 'notochord,' and the first has a pair of gill slits. In other respects these are strikingly Polyzoan in appearance.

SUB PHYLUM IV. VERTEBRATA.

In the vertebrates only the internal segmentation occurs. This is shown, and most clearly, in the lower Vertebrata, in the muscles (myotomes, myomeres), the myocommata or myosepta which separate them, and the protovertebræ from which they arise; in the nerves (neurotomes), the skeleton (sclerotomes), the blood-vessels, and in the excretory organs (nephrotomes). In the higher vertebrates this metamerism is visible only in the embryonic stages. In part this absence of external segmentation has its cause in the heteronomy (p. 399) of the body and the obliteration of segmental boundaries, consequent upon the union of somites into body regions, of which at least three—head, trunk, and tail—at most six—head, neck, (cervical) thorax, lumbar, pelvic (sacral), and tail (caudal)—occur. Not less important in this respect is the character of the skeleton. The cuticular skeleton, which is the cause of the annulation of the arthropod, is entirely lacking. The skin remains soft, or contributes to a subordinate degree, more for protection than for support, to the formation of a skeleton (dermal skeleton of fishes, alligators, turtles). On this account firmer tissue is formed in the axis of the body, which, in the lowest vertebrates and the embryos of the higher, appears as the notochord already mentioned, but in the higher is supplemented by the vertebral column and skull.

The skin of the vertebrates is distinguished from that of all invertebrates by two characters (figs. 26, 27): the many-layered condition of the epidermis, and the considerable thickness of the derma. The epidermis is but rarely covered by a delicate cuticle; usually such a protection is unnecessary since—and especially in the land forms—the superficial layers become cornified and hence furnish the necessary resistance without a cuticle. There are two layers to be distinguished, the deeper stratum Malpighii and the superficial stratum corneum (*sM* and *sc*; see p. 76).

The second constituent of the integument, the derma (cutis, corium), arises from the mesoderm (mesenchyme). It consists of many layers, often stratified, of close connective tissue, and is usually separated from the underlying structures, especially the muscles, by a loose tissue rich in lymph spaces, the subcutaneous tissue. Both of these constituents of the skin, aside from their own firmness, can give rise to protective structures. The horny layer of the epidermis in places becomes greatly developed and thus forms the tortoise shell of the turtles, the scales, shields, and scutes of the snakes and lizards, the feathers of the birds, the hair and horns of the mammals. Other epidermal products are the claws, nails, and hoofs of the terrestrial vertebrates. The derma is often the seat of ossifications which, in contrast to the deeper bones, are called the dermal skeleton.

First of the dermal skeletal parts are the scales of the fishes, which, in spite of similarity of name, are different from the epidermal scales of the reptiles. They may be traced back to the primitive form, the placoid scales of the Elasmobranchs. These are rhombic plates, bearing in the middle pointed spines, which are called dermal teeth from similarity in structure and development to the teeth of the mouth cavity (fig. 554). They consist of dentine (*d*) and have a large pulp cavity (*p*), with numerous blood-vessels in the interior. Whether the thin layer (*sch*) covering the tip can be called enamel is disputed. Dermal teeth and true teeth are identical structures which, in consequence of different position and consequent difference of function, have developed differently.

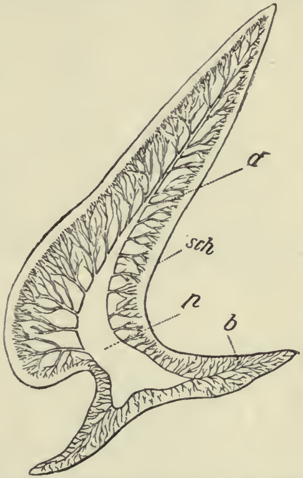


Fig. 554.—Sagittal section of a scale of *Scyllium stellare*. (After Hofer.) *b*, basal plate; *d*, dentine; *p*, pulp cavity; *sch*, enamel.

The scales of fishes have a wider anatomical interest, since from them have arisen, besides the bony plates which form the resistant armor of the turtles, alligators, and many mammals (Armadillos), important parts of the axial skeleton, the secondary or membrane bones. A membrane bone is a bony plate which has arisen from a fusion of dermal ossifications, becomes transferred to a deeper position, and contributes to the completion of the axial skeleton. After what was said above about the relations of dermal and true teeth it is readily seen that a further source of formation of membrane bones lies in the lining of the mouth cavity.

In describing the axial skeleton, the notochord comes first. This has already been mentioned in connexion with the lower Chordates. It persists in the cyclostomes, but from them upwards it is gradually replaced by the vertebræ arising around it. It is of entodermal origin (fig. 9), arising as a longitudinal band of the epithelium of the archenteron (*I, ch*), and, becoming cut off, comes to lie in the long axis of the body between digestive tract and nervous system (*II, III*); here it forms a cylindrical rod consisting of a connective tissue which, as already said, resembles plant tissues because of the vesicular nature of its cells (fig. 38).

In transverse section (fig. 555) the chorda is surrounded by three layers, internally by a fibrous notochordal sheath, then an elastic layer (not always present), the elastica externa, so called because an elastica interna is sometimes present inside the notochordal sheath; and lastly a skeletogenous layer (*SS*), also called the outer notochordal sheath. This last is a mesodermal connective-tissue layer and is therefore connected with the other connective-tissue sheaths which surround muscles, nerves, etc., and deserves special mention because in it the cartilages and bones arise from which the vertebræ and skull are formed. Cells from it can penetrate the notochordal sheath, converting it into fibrous cartilage, thus enabling it to participate in the formation of the vertebræ.

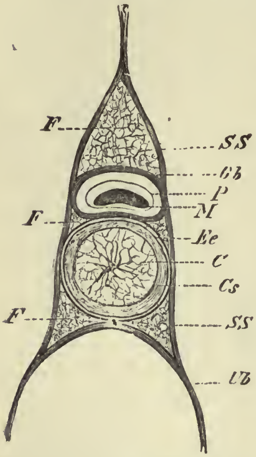


Fig. 555.—Transverse section of axial skeleton of *Petromyzon*. (From Wiedersheim.) *C*, notochord; *Cs*, notochordal sheath; *Ee*, elastica externa; *F*, fatty tissue; *M*, spinal cord; *P*, its meninges; *Ob*, upper process of skeletogenous tissue; *SS*, skeletogenous tissue; *Ub*, lower process of skeletogenous tissue.

Since the notochord and its sheaths are elastic and give under the strain of the muscles, they are unsegmented. The segmentation of the axial skeleton begins with the appearance of firmer tissue in cartilage and bone. Then there is a separation of successive parts, and with this the gradual formation of vertebral column and skull. For both there is a connected series of developments, if studied with reference to the ontogenetic processes or in the comparative manner from the lower to the higher forms.

The first parts of the vertebral column to appear are the upper and lower (figs. 555, 556), or *neural* and *hæmal arches*. These consist of paired parts in the skeletogenous layer which abut against the notochord, and which are usually a pair to the somite, although occasionally two or more pairs, the arches proper and the *intercalaria*, may occur. The neural arches (arcus vertebræ of human anatomy) enclose a *spinal canal* surrounding the spinal cord, the parts of the arch, *neurapophyses,* uniting above the cord to form the *spinous process* (frequently an independent part of the skeletal axis). In the caudal region, in the same way, *hæmal arches* may be formed of *hæmapophyses* and *hæmal spine,* the arches surrounding the blood-vessels of the tail (fig. 557). In the trunk region the ventral arch behaves differently. Since the large body cavity with its viscera, varying in size (digestive and reproductive organs), is here, the hæmapophyses extend outwards and downwards and are divided into two parts, a basal *apophysis* and a lower movable portion, the *rib* (fig. 556). Also the lower union of hæmapophyses with hæmal spine does not occur; the ribs are either free (fishes) or are (at least in part) connected ventrally by

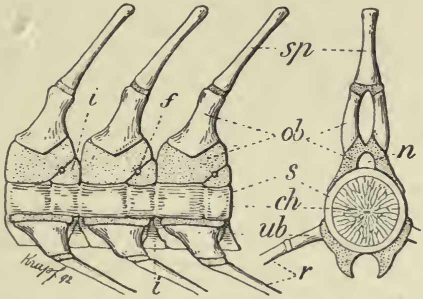


FIG. 556.—Vertebræ of sturgeon. *ch,* notochord; *f,* exit of nerve; *i,* dorsal and ventral intercalaria; *n,* neural canal; *ob,* neural arch; *s,* chordal sheath; *r,* rib; *ub,* hæmal arch. Bone white, cartilage dotted.

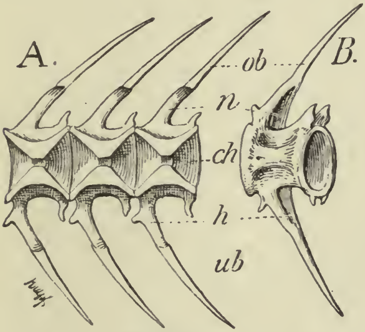


FIG. 557.

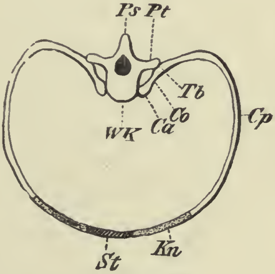


FIG. 558.

FIG. 557.—Caudal vertebræ of a carp, section (*A*) and nearly side view (*B*). *ch,* space filled by notochord; *h,* hæmal arch; *n,* neural arch; *ob,* neural spine; *ub,* hæmal spine.

FIG. 558.—Thoracic vertebra, ribs, and sternum of a mammal. (From Wiedersheim.) *Ca,* capitular head of rib; *Co,* neck of rib; *Cp,* bony rib; *Kn,* cartilaginous rib; *Ps,* spinous process; *Pt,* transverse process (diapophysis); *St,* sternum; *Tb,* tubercular head of rib; *WK,* vertebral centre.

a breast bone or *sternum* (Amniotes, fig. 558). The sternum is a derivative of the ribs. In development the ventral ends of the ribs of a side fuse and then these fused tracts of the two sides unite to form the sternum.

The hæmal arches lie internal to the longitudinal muscles of the body, and in the trunk region they lie in the same position just beneath the peritoneum. These are *hæmal ribs* and are found only in teleosts and ganoids. The ribs of all other vertebrates (elasmobranchs, amphibia, amniotes) are morphologically different and are called lateral or *pleural ribs*. They develop independently of the vertebral column in a horizontal connective-tissue septum which extends out through the longitudinal muscles from the axial skeleton to the skin, dividing the musculature into dorsal (epaxial) and ventral (hypaxial) portions (fig. 89). In the elasmobranchs these pleural ribs are attached to the hæmapophyses, in the others to the transverse processes (*diapophyses*), which arise from the neurapophyses, and *parapophyses*, which arise from the vertebral centres. In the caudal region, often also in the cervical, lumbar, and sacral regions, the pleural ribs and dia- and parapophyses fuse to form lateral processes. These occur concurrently with hæmal arches in the tails of many Amphibia and reptiles and some mammals, forming the *chevron bones* which, as in fishes, enclose the caudal blood-vessels. The presence of intercalaria in cyclostomes, sharks, and ganoids indicates that primitively a double vertebra arose in each somite. Paleontological and embryological researches on reptiles support this view.

In most vertebrates either the basal ends of the arches broaden out around the notochord and fuse with one another, or perichordal cartilages arise independently, furnishing in either case firm supports, the vertebral bodies, or *centra*, for the system of arches. These increase in size at the expense of the notochord on the inside, sometimes leading to its almost complete obliteration, as in the mammals; in others, as the fishes, the reduction is less complete. The fishes have *amphicœle* vertebræ (fig. 557), that is, the centra are hollow at either end. In these cups the notochord exists even in the adult, and when small connecting portions extend through the centra the notochord takes the form of a rosary with alternating enlargements and contractions.

Histologically the vertebral column may be either cartilage or bone; usually it is first formed in cartilage, which is later replaced by bone. If the ossification does not occur, the column remains cartilaginous; if incomplete, cartilage and bone appear side by side. Since these histological differences are combined with varying degrees of persistence of the notochord and with modifications in the form of the vertebræ and their processes, there results an extraordinary variety in the appearance of the vertebral column.

In order to allow for bending where complete centra are present various conditions occur. (*a*) *Opisthocœle* vertebræ have a socket on the hinder surface which receives the convex anterior end of the succeeding centrum, forming a ball-and-socket joint. (*b*) *Procœlous* vertebræ have these relations reversed, the socket being in front. (*c*) The vertebræ may articulate with a 'saddle joint' (birds). (*d*) Between two successive vertebræ an elastic intervertebral ligament may occur (mammals). The neurapophyses may bear, in addition to the transverse processes, anterior and posterior articulating processes (zygapophyses) connecting the separate vertebræ.

The skull, the anterior continuation of the axial skeleton, occurs in all vertebrates; it appears before the vertebræ, for it is found in the cyclostomes, which lack these. It surrounds the brain as the vertebræ do the spinal cord; and, like them, its first stages are formed in the skeletogenous layer surrounding the anterior end of the notochord. It is so related to the surrounding parts that it may in general be said to be equivalent or homodynamous with the vertebræ, although we cannot agree with Oken and Goethe, the founders of the vertebrate theory of the skull, that it has arisen by the fusion of vertebræ. On the other hand skull and vertebræ are parts arising in the common basis of the skeletogenous layer, but which have developed in different directions.

Three stages are recognized in the development of the skull: the membranous, the cartilaginous cranium, and the bony skull. The first, which consists of connective tissue, occurs only in the early embryonic stages, scarcely a trace of it persisting in the adults. It is early replaced by the cartilaginous skull, which may persist unaltered throughout life in the lower fishes (elasmobranchs, sturgeon). In most vertebrates, however, ossification sets in, embracing a part (fishes, amphibians) or the whole of the cartilage (birds, mammals), converting it in the latter case into a bony capsule. In the bony skull two kinds of bone, primary and secondary, are recognized, these varying in their origin. The primary or cartilage bones develop from the cartilage itself, either in its interior (*entochondrostoses*) or in its enveloping perichondium (*ectochondrostoses*). The secondary or membrane bones are, in their origin, foreign to the axial skeleton and arise from the ossifications in the skin (scales) or in the mouth (teeth), already referred to (p. 515). They sink into the deeper portions and apply themselves to the axial skeleton, especially to those parts where, from lack of cartilage, no primary bones can be formed (*parostoses*). Still it is not settled how far these distinctions may be carried. According to Gegenbaur all ossifications arose primarily in the skin or mucous membranes, and primary bones are merely membrane bones which have entered the cartilages and replaced them. According to this view it is conceivable that the same bone in one animal may arise as a membrane bone and in another as a primary bone, a view which is of importance in the homologies and nomenclature of many bones. It is but just to say that this view is not universally accepted.

The cartilaginous cranium (*chondrocranium*) is most complete beneath the brain. This basal portion is a direct continuation of the vertebral column, and a part of it (the *parachordals*) embraces the anterior end of the notochord, while part (the *trabeculæ*) extends in front of the end of the notochord. The side walls of the skull are increased by the cartilaginous envelopes of the two sense organs, the nasal and otic capsules, around the nose and ear. Between these is a hollow for the eye which contributes nothing to the skull. In only a few forms is the chondrocranium completely

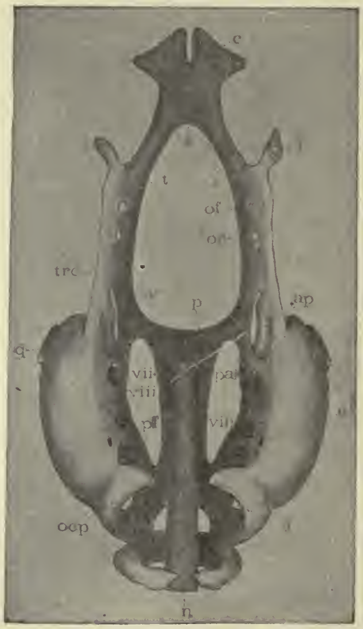


FIG. 559.—Chondrocranium of *Amphiuma*. *anp*, antorbital process; *ap*, ascending process of quadrate; *c*, cornu trabeculæ; *e*, ethmoid plate; *ef*, endolymph foramen; *j*, jugular foramen; *l*, lamina cribrosa; *m*, Meckel's cartilage; *n*, notochord· *oc*, oculomotor foramen; *ocp*, occipital process; *of*, optic foramen; *p*, parachordal; *pal*, palatine foramen; *pf*, perilymphatic foramen; *q* quadrate; *s*, stapes; *sp*, stapedial process; *t*, trabecula; *trc*, crest of trabecula; *V*, *VII*, *VIII*, foramina for *V*, *VII*, *VIII* nerves.

closed; usually gaps (*fontanelles*) occur in its roof, and frequently in its floor. The higher the animal intellectually and the larger its brain the more the connective tissue (*primordial cranium*) is called upon to roof in the chondrocranium. Hence it is that in the reptiles, birds, and mammals, where it is also confined to embryonic life, the chondrocranium is relatively the smallest. Since it only closes above in the occipital (hinder) region, while it gaps widely in front, it follows that the secondary bones play an important part in the completion of the skull.

The bony skull presents great difficulties from the standpoint of comparative anatomy, in part from its varying appearance in the different groups, in part on account of the number and complicated arrangement of the constituent bones. It may be said in beginning that as a rule the same bone reappears in the separate classes, and that the difficulties are connected with the fact that certain bones may fail to develop (Amphibia), or they may fuse to larger elements (mammals). A further complication results from the intimate union with the cranium of bones of the visceral arches, which, strictly speaking, do not belong to it.

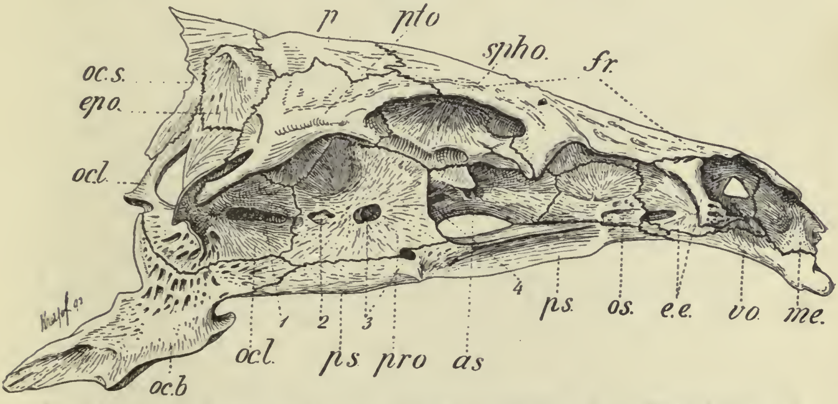


Fig. 560.—Skull of carp, the visceral skeleton removed. (A) Cartilage bones: *ocb ocl*, *ocs*, basi-, ex-, and supraoccipitals; *epo*, epiotic; *pto*, pterotic; *spho*, sphenotic; *pro*, prootic; *as*, alisphenoid; *os*, orbitosphenoid; *me*, mesethmoid; *ee*, ectethmoid. (B) Ventral membrane bones: *ps*, parasphenoid; *vo*, vomer. (C) Dorsal membrane bones: *p*, parietal; *fr*, frontal; *1-4*, exits of nerves.

The primary bones (preformed in cartilage) can be divided according to the cranial regions into four groups: (1) bones of the hinder part of the head—*occipitalia;* (2) bones of the ear region —*otica;* (3) bones near the eye—*sphenoidalia;* and (4) of the nasal capsule—*ethmoidalia*. The occipitalia—four in number (figs. 560–562)—united in the higher mammals to a single occipital bone, surround the foramen magnum, the opening through which the spinal cord passes to connect with the brain. These are a pair of exoccipitals, right and left, a supraoccipital above and a basioccipital below. The otica depend in their development upon the extent of the otic region. In the fishes, where this part is large, several bones may be present: epiotic, pterotic, sphenotic, prootic, and often opisthotic. In the mammals, on the other hand, these are fused to a single petrosal bone (figs. 561, 562) of small size.

Since the otic bones usually do not reach the middle line below, the sphenoidalia rest direct upon the basioccipital behind and in front upon a presphenoid bone, both unpaired but arising from paired centres. With each is connected, right and left, a pair of bones; with the basisphenoid the alisphenoids, with the presphenoid the orbitosphenoids, just as the exoccipitals flank the basioccipital. In the region of the nasal capsule there is an unpaired mesethmoid with a pair of ectethmoids. Hence the cranium of primary bones may be described as a chain of four median basal bones, basioccipital, basisphenoid, presphenoid, and mesethmoid; right and left of this a row of exoccipital, alisphenoid, orbitosphenoid, and ectethmoid. The position of the otic capsule results in the sum of the otic bones, the petrosal, being wedged in between the exoccipitals

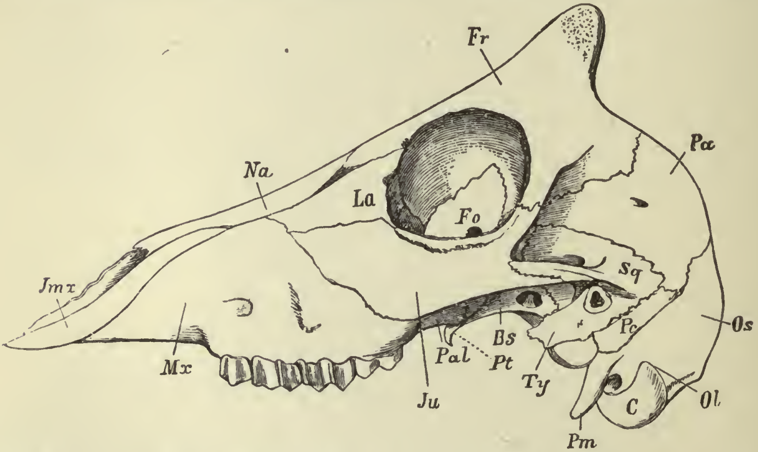


FIG. 561.—Skull of goat. (From Claus.) *Als*, alisphenoid; *Bs*, basisphenoid; *C*, occipital condyle; *Eth*, mesethmoid, covering the ectethmoid; *Fo*, optic foramen in orbitosphenoid; *Fr*, frontal; *Imx*, premaxillary; *Ip*, interparietal; *Ju*, jugal (malar); *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Ob*, basioccipital; *Ol*, exoccipital; *Ors*, orbitosphenoid; *Pa*, parietal; *Pal*, palatine; *Pe*, petrosal; *Pm*, paramastoid process; *Ps*, presphenoid; *Pt*, pterygoid; *Sf*, frontal sinus in frontal bone; *Spb*, basisphenoid; *Sq*, squamosal; *Ty*, tympanic; *Vo*, vomer.

and the alisphenoid. Only behind is there a dorsal element, the supraoccipital.

The skull must be roofed in by membrane bones, and of these three pairs are almost constantly present. These are, from behind forwards, a pair of parietals, a pair of frontals, and a pair of nasals, the latter covering the nasal capsules. Confined to the lower vertebrates is a large membrane bone on the floor of the skull, the parasphenoid, which reaches from the basioccipital to the mesethmoid.

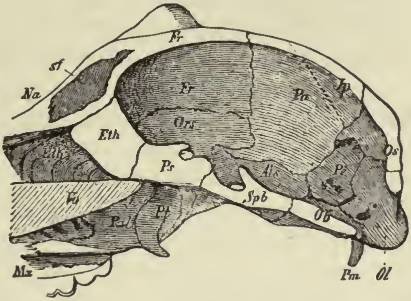


FIG. 562.—Sagittal section of hinder part of goat skull. (From Gegenbaur.) For lettering see fig. 561.

The scheme of the cranium thus outlined undergoes the most modifications in the sphenoidal region. Parasphenoid, on the one hand, and basi-and presphenoid, on the other, may be substituted for one another, so that when the parasphenoid is present (fishes, Amphibia) the others are small or absent and *vice versa* (mammals). In the mammals, besides, the alisphenoids fuse with the basisphenoid (greater wings), the orbitosphenoids with the presphenoid (lesser wings), so there arise here an anterior and a posterior sphenoid, fused in man to a single sphenoid bone. Mesethmoid and ectethmoids likewise fuse in the mammals to an ethmoid bone.

The brain case, or cranium, is developed into the complete skull by the addition of the visceral skeleton, a series of arches which, like ribs, embrace the beginning of the alimentary tract and are related to the cranium, much as are ribs to the vertebræ. These must be considered as parts of the skull, although in part they are shoved backwards and lie under the anterior end of the vertebral column. As the ribs arise in alternation with the musculature (*myomeric*), so the visceral arches are similarly related to the gill formation (*branchiomeric*). Analogous to the cranium the visceral skeleton has a cartilaginous and a bony stage. The visceral skeleton is entirely cartilaginous only in Elasmobranchs, and here it is so loosely connected with the cranium as to be easily separated from it. It consists in these forms usually of eight (rarely eleven) arches (fig. 588); these are, from in front backwards, the rudimentary labial cartilages, then the large *mandibular arch*, the *hyoid* arch, and five (rarely seven) gill or *branchial arches*. The mandibular arch consists, on either side, of two pieces which bear teeth and oppose each other in biting; the upper half, attached to the skull in front and behind, is the *pterygoquadrate* (is not the upper jaw of higher forms). The lower part, which is hinged to the other, is the *mandibular* or Meckel's cartilage. In the same way the hyoid arch is divided into an upper, or *hyomandibular*, and a lower hyoid proper on either side, the hyomandibular being fastened to the otic capsule. The hyoids are united below by an unpaired piece, the *copula*. A copula also exists between the halves of the branchial arches, each of which consists of four parts on either side. Hyoid and gill arches bear gills. Certain features (existence of rudimentary gills and a rudimentary gill cleft, the spiracle) indicate also that the mandibular arch was once gill-bearing and that it lost its original function upon being converted into an organ of mastication. Recently the labial cartilages have been regarded as remnants of a support for tentacles around the mouth like those of *Amphioxus* and *Myxine*, and which reappear anew in the barbels of bony fishes. Hence they are not comparable to the other arches.

By ossification the visceral arches of the higher fishes and all higher vertebrates produce a great modification of the skull, this being increased by a progressive change of function of the arches, which depart more and more from their relations to the respiratory apparatus. From this standpoint they may be divided into two groups, an anterior, consisting of labial cartilages, mandibular arch, and the hyomandibular; and a posterior, of the hyoid and the gill arches. The hinder arches are well developed as long as branchial respiration persists. With the loss of gills they largely disappear, but what remains forms the hyoid or tongue bone (not to be confused with the hyoid proper), its body being composed of the copula, its anterior horns of the hyoid, and its posterior horns of the remnants of a gill arch. Other gill arches contribute to laryngeal cartilages, the epiglottis and the cartilages of the auditory meatus.

The anterior members of the visceral skeleton (labials, pterygoquadrate, Meckelian, and hyomandibular) become developed further, but lose more and more their individuality and unite with the cranium; in the mammals forming the 'bones of the face.' It is therefore a source of additional bones which are difficult to follow from class to class, since they change in their functions and consequently in shape and relative size.

All vertebrates with bony visceral skeleton (figs. 561, 589) have two pairs of membrane bones, right and left, in front of the pterygoquadrates, the premaxillaries (intermaxillaries) and maxillaries. They bear, in toothed vertebrates, the marginal row of teeth, which are distinguished from the palatopterygoid teeth in that they are opposed by the teeth of the lower jaw. The pterygoquadrates are thus forced backwards and form a second series of bones, parallel to the maxillary series, which likewise may bear teeth. This row of bones consists of an anterior palatine portion and a posterior quadrate part. The cartilages of the palatine part largely disappear and are replaced, in front, by a pair of vomers followed by a pair of palatines, while farther back are a pair of pterygoids. The quadrate portion ossifies into the quadrate bone, which affords the articulation for the lower jaw. The ossifications for the lower jaw occur in a similar way; in front a series of membrane bones, of which the dentary is most important, surrounding Meckel's cartilage, while the hinder part of the Meckelian ossifies into the articulare, so called because it articulates with the quadrate. The hyomandibular forms only one constantly present bone known by the same name.

If all vertebrates with bony skeletons be compared, it is found that those with terrestrial habits have a sound-conducting apparatus in connexion with the ear. This is composed of elements which, in the fishes, lie in the neighborhood of the otic capsule, the hyomandibular, the quadrate, and the articulare, to which is added another element, the stapes, which occupies the fenestra ovalis (p. 544) and is derived from the otic capsule itself. In Anura, reptiles, and birds the hyomandibular apparently gives rise to an element, the columella, which abuts against the stapes. In the mammals stapes and columella are possibly fused, while quadrate and articulare undergo a change of function, losing their position in connexion with the articulation of the jaws and being converted into part of the sound-conducting apparatus, the quadrate furnishing the incus, the articulare the malleus (figs. 576, 577). Since the lower jaw in this way loses its articulation, a new one is formed by a process from the membrane bones.

According to this view the lower jaw of a mammal is not equivalent to the lower jaw of a bird, since in the latter the hinge is furnished by the quadrate-articulare joint. It should be said that another view obtains, though not so well supported, which considers the ear bones as exactly homologous throughout terrestrial vertebrates, and which recognizes incus and malleus in the columella and maintains that quadrate and articulare form the hinge of the mammalian jaw.

In conclusion three other bones, widely distributed, must be mentioned—the squamosal, the tympanic, and the jugal. The squamosal is a membrane bone arising at the boundary of quadrate and otic capsule (petrosal), and hence with relations to both these bones. It increases in size as the quadrate diminishes in changing to the incus, and in the mammals fuses with the petrosal to form the temporal bone. In common with the tympanic, which in mammals also fuses with the petrosal, it forms a frame for the attachment of the tympanic membrane of the ear. The jugal (malar, zygomatic) belongs to the maxillary series. In many vertebrates this series is articulated only in front, its posterior end terminating freely in the soft parts, but when the jugal occurs it forms a jugal or zygomatic arch which bridges the gap between the maxillary and the quadrate region of the skull. When the quadrate becomes modified to the incus, the jugal articulates with its companion, the squamosal, which extends a zygomatic process forward for this purpose.

Difficulties in ascertaining the morphological relations of bones arise where the visceral and cranial parts join and where primary and secondary bones touch, especially since in the latter no general criteria of distinction can be drawn. Thus the pterotic, sphenotic, and ectethmoid of the fishes are often replaced by other secondary bones in the Amniotes; the primary pterotic by the secondary squamosal; the primary sphenotic and ectethmoid by two membrane bones in front of and behind the frontals, the prefrontals and postfrontals of reptiles and other forms.

Just as skull and vertebral column form a firm axis for the body, the appendages are supported by axial skeletal structures. Two kinds of appendages are recognized, paired and unpaired, which generally occur together only in fishes (figs. 598–608). The unpaired consist of a fold of the skin beginning in the sagittal plane behind the head, running back around the tail and forward on the ventral surface to the anal region. This continuous fold is nearly always divided into three parts, a dorsal fin (often subdivided into smaller fins), a caudal fin, and an anal fin. In a similar way, apparently, the paired appendages—an anterior or thoracic and a posterior or pelvic pair—have arisen from a pair of continuous folds, by development of the appendages themselves and suppression of the intermediate regions. Of these the unpaired are possibly the oldest, since they occur not only in the cyclostomes, but in *Amphioxus* and the tunicates as well, where paired appendages are lacking; on the other hand they disappear in the higher forms. Since they are of service only in an aquatic life, they are lost in the Amphibia, in which a continuous fin, unsupported by skeletal elements, occurs only in larval life. On the other hand the paired appendages gain in importance with terrestrial habits.

In the fins of fishes two kinds of skeletal elements occur which, in the Elasmobranchs, are distinguished by their histological structure, since the one, the fin supports (basalia and radialia), consist of cartilage, the others (actinotrichia, dermal skeleton) are of horny consistency (fig. 563). Since in the teleosts both kinds of supports may ossify, the distinction is here less striking, yet the basalia and radialia arise from cartilage and lie in the basal part of the fin, while the others are never cartilaginous and occur in the distal portion. These distinctions are of importance, since the actinotrichial portions play no part in the development of the extremities of the higher groups. These arise from the basal supports of pectoral and pelvic fins, which therefore alone need further mention.

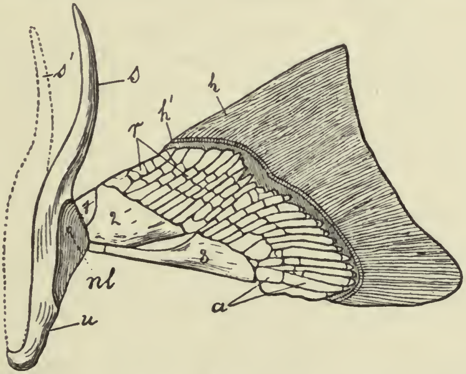


FIG. 563.—Pectoral girdle and left fin of *Heptanchus*. (After Wiedersheim.) *a*, principal row of the cartilaginous fin supports; *h*, horny threads or fin rays cut across at *h'*; *nl*, foramen for nerve; *r*, accessory cartilaginous fin supports; *s*, *s'*, scapula; *u*, ventral portion of girdle.

The skeleton of the paired appendages, preformed in cartilage, consists of two parts, the girdles lying in the lateral walls of the trunk, and the skeleton of the limbs themselves. A girdle—a shoulder or pectoral girdle in front, a pelvic girdle for the hind limbs—is in its simplest form an arch with right and left halves, each half with an articular surface for the limb, dividing it into dorsal and ventral portions (fig. 563). The dorsal portion is the scapula (shoulder blade) in the pectoral, ilium in the pelvic girdle. The lower portion is usually split into anterior and posterior parts (fig. 564). The anterior of these is the clavicle in the pectoral girdle, pubic bone in the pelvis; the hinder part is the coracoid or the ischium in the two girdles respectively. These parts are most constant in the pelvic girdle. In the pectoral girdle either coracoid or clavicle may be lacking, at times both are absent; but no vertebrate with fore limbs lacks a scapula. In the clavicle there is frequently an element, preformed in cartilage, the procoracoid, to be distinguished from a membrane bone, the clavicle in the strict sense.

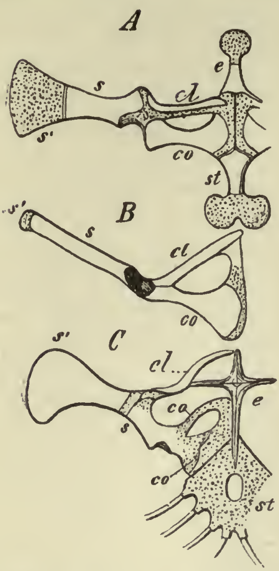


FIG. 564.—Right half of shoulder girdles of (*A*) frog, (*B*) turtle, (*C*) lizard. (After Gegenbaur, slightly modified.) *cl*, clavicle; *co*, coracoid; *e*, episternum; *s*, scapula; *s′*, suprascapula; *st*, sternum, in *C* with bases of ribs.

In the fishes the girdles are largely or entirely held in position by muscles; in most terrestrial vertebrates there is a more intimate connexion with the axial skeleton and especially with the vertebral column. In the case of the pelvic girdle the connexion is direct, since the ilium is articulated with one or more sacral vertebræ (in reality not with the vertebræ themselves, but by the intervention of sacral ribs). The connexion of the pectoral girdle is less direct and is looser. This is effected by clavicle and coracoid. The latter connects with the sternum, which in turn is connected to the vertebral column by the ribs; the clavicle articulates with a bone, the episternum, which rests upon the breast bone, the morphological relation of which is doubtful, since under this term have been included different structures (the membrane bone of Reptiles, episternum in the strict sense, the cartilage bone, the prosternum of the monotremes and the præclavia of the mammals).

Since only the free portions of the appendages are concerned directly in locomotion, and since the various modes of motion—swimming, flight, running, leaping, climbing—demand special modifications, the skeleton of the limbs shows great variety. It is usually believed that all these forms are to be traced back to an ancestral type, the archipterygium. In this (fig. 563) are numerous skeletal parts which vary little in size and form and are arranged in many closely appressed rows. One of the rows has acquired prominence and is called the principal row; it begins with a larger piece, the metapterygium, which articulates with the girdle and bears either on both sides (archipterygium biseriale) or only on one (archipterygium uniseriale) the lateral rows of skeletal elements. Usually most of the lateral rows are not attached to the principal row, but arise independently from the girdle, and may begin with larger parts, the propterygium and mesopterygium.

From this archipterygium can be derived a primary form which serves for all terrestrial vertebrates from the Amphibia onwards; it is the pentadactyle appendage (fig. 565). In tracing this from the archipterygium (of either uniserial or biserial type) the following modifications must be supposed. First a reduction in the number of rows to five, a principal row and four accessory rows. The terminal portions of the principal row produce the bones of the fifth, the accessory rows of the other fingers. Then there is an unequal growth of parts; the metapterygium, already in Elasmobranchs a considerable element, increases in size and forms in the fore limb the humerus, in the hind limb the femur. In like manner the second element of the principal row and the first of the first accessory row increase and form respectively ulna and radius in front, fibula and tibia behind. Then follow parts which remain small and somewhat cubical, carpal bones in the fore limb, tarsals in the hinder extremity; they bear in turn slender bones, the metacarpals or metatarsals, and these at last the phalanges. (For the nomenclature of carpals and tarsals see the explanation of fig. 565.)

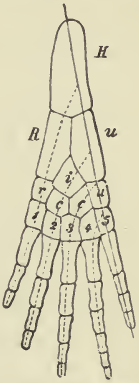


Fig. 565.—Schema of a pentadactyle appendage. (After Gegenbaur.) The dotted lines indicate the lateral rays; the names for the hinder extremities in parentheses. *H*, humerus (femur); *U*, ulna (fibula); *R*, radius (tibia). Carpus (tarsus) consisting of two rows and two central portions: Row I: *r*, radiale (tibiale); *i*, intermedium; *u*, ulnare (fibulare); *c*, centralia. Row II: *1–5*, carpalia (tarsalia); the metacarpals (metatarsals) and phalanges not lettered.

The third and most important modification is brought about by the development of joints. So long as the appendage served as an oar it must act as a single plate with its parts firmly held. On the other hand, when it must act as a system of levers to support and move the body, as is necessary in a terrestrial animal, it must be divided into sections, jointed to each other. By this there are developed two joints of importance in both fore and hind limbs; the elbow (knee) joint between humerus (femur) on the one hand and radius and ulna (tibia and fibula) on the other; and the wrist joint (ankle) between the bones of the fore arm (shank) and the carpals (tarsals). Less important are the joints of the fingers and toes.

If the limbs of terrestrial vertebrates be compared with this primary form, variations are seen in two directions. Rarely are there more bones than in the schema; then there occur remnants of a sixth or even a seventh row or finger. More frequently there is a reduction in the number of parts, either by fusion or by absolute loss. Fusion accounts for the fact that with complete pentadactyly the number of carpalia is usually less than ten, as would be expected from the schema. Degeneration and loss explain the existence of animals with four, three, two, or even one digit, and one can say with certainty that the missing parts are in most cases lost, though a fusion of digits is not unknown. Paleontology, for example, teaches that the one-toed horse has descended, by gradual reduction, from five-toed ancestors.

The completeness and character of the skeleton thus sketched in outline has a great influence on the rest of the organism. It has already been pointed out that the external appearance of vertebrates has been influenced by it, since the skin is no longer, as in arthropods, a supporting structure and has consequently lost its segmentation. More immediate is its influence upon the arrangement of the musculature. The development of an internal skeleton renders it necessary that the point of resistance of the muscles

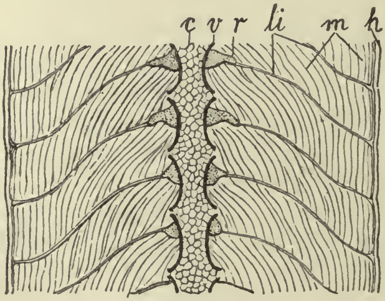


Fig. 566.—Horizontal section through the anterior trunk region of a young *Rhodeus amarus* at the level of the ventral arches. *c*, notochord; *h*, skin; *li*, intermuscular ligament; *m*, longitudinal muscles; *r*, rib end of the cartilaginous ventral arch; *v*, osseous centrum.

must be transferred from the skin, where it is found in annelids, molluscs, and arthropods, to the interior. A dermal musculature occurs only as an inconspicuous remnant in vertebrates; it is replaced by a body musculature. This latter consists primarily of a longitudinal system of muscle fibres on either side of the vertebral column (fig. 566), which are divided by connective-tissue partitions, the myosepta or myocommata, into successive segments, the myotomes. Thus when the connective tissue of a fish is dissolved by cooking the muscles fall into disk-like parts. The myosepta extend from skin to axial skeleton. Since they run obliquely backwards from the skeleton to the skin, they serve to render the skeleton a point of resistance for the action of the muscles.

A segmented trunk musculature occurs in the Myxinoids (and in *Amphioxus*), in which the axial skeleton consists only of notochord and is consequently unjointed. The segmentation of the muscles is therefore older than that of the skeleton and, as we can further say, is the cause of it. The action of the muscles prevents the formation of a cartilaginous or bony vertebral continuum such as the notochord and skeletaginous layer are. It produces at intervals joints or flexible parts separating the cartilaginous or bony column into vertebræ. Naturally these flexible portions cannot coincide with the boundaries of the muscles, but must lie between them; in other words, muscle segments and skeletal segments—myotomes and sclerotomes—must alternate. Segmentation is lacking in the cranium, since the myotomes here have no locomotor significance, are reduced, and only small remnants of them persist.

In the mammals only a little of this segmental arrangement of muscles is recognizable, a result of the development of the appendages; and the more these gain in importance as the locomotor structures, the more the muscles are modified and grouped for the service of the limbs, so that only the intercostals and a part of the muscular system to the sides of the vertebral column show clearly the primitive metamerism. Yet in all vertebrate embryos the muscles appear at first strictly segmental, in the form of the primitive somites (fig. 567), formerly called protovertebræ.

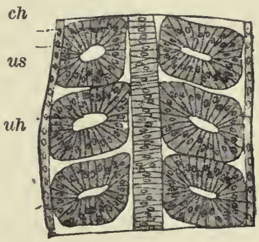


FIG. 567.—Horizontal section of an embryo of *Triton*. (From O. Hertwig.) *ch*, notochord; *uh*, myocœle; *us*, primary muscle segment (myotome).

Another important point in the musculature lies in the fact that it is dorsal in origin and therefore in fishes is largely dorsal in position throughout life. The muscles which are ventral have largely been transferred from the back, and the cause of the migration is to be recognized to a large extent in the progressive development of the appendages. The dorsal position of the muscles is only a part of a general fact, that the skeletal axis divides the body into a dorsal zone, containing only animal organs, and a ventral zone, chiefly vegetal in character. Besides, the muscles, the central nervous system, and the most important sense organs—eyes, nose, ears—belong to the dorsal zone.

The central nervous system of vertebrates consists of brain and spinal cord. Like that of all chordates it is distinguished from that of other segmented animals—annelids, arthropods, in which there is a dorsal brain and a ventral nerve chain—in its purely dorsal position. It is further distinguished from that of all non-chordates by its tubular character, that is, by the presence of a central canal in the axis of the elongate central system (fig. 76), lined by a special epithelium, the ependyma, and containing a fluid, the liquor cerebrospinalis. This central canal is the result of the mode of development, the nervous system arising by an inrolling of the ectoderm and not by a splitting from it as in the invertebrates (fig. 9). Besides the neurenteric canal already referred to (p. 502), there long persists at the anterior end an opening to the exterior, the neuropore. In all vertebrates, in contradistinction to the lower chordates, the brain is large and sharply marked off from the spinal cord.

The spinal cord is a cylindrical structure (flattened in Cyclostomes, fig. 555) which, in the middle line above and below, is marked by two longitudinal grooves, the dorsal and ventral fissures of the cord (*sp*, *sa*, fig. 76). The central canal (*Cc*) has its lumen greatly narrowed by the growth of the nervous tissue, in which, as in the ganglia of the invertebrates, two layers are distinguished, one containing almost solely nerve fibres, the other both fibres and nerve or ganglion cells. The arrangement of these layers is contrasted with that of the invertebrates in that the ganglion-cell layer—the gray matter—lies in the centre, the fibrous layer—white matter (*W*)—on the periphery, a reversed position consequent upon the development by infolding. The distinction in color indicated in the names depends upon the fact that white medullated fibres run in the cortex, while in the gray matter gray non-medullated fibres are present between the nerve cells. The color distinctions fail in the cyclostomes (and *Amphioxus*), which have no medullated fibres, although the same general structure occurs.

The gray matter surrounds the central canal, but extends on either side dorsally and ventrally into the white matter, so that in section it resembles somewhat the letter H, with its dorsal (fig. 76, *HH*) and ventral horns (*VH*). By means of these horns and the dorsal and ventral nerve roots arising from them, the white matter on either side is divided into three tracts, the dorsal (*H*), ventral (*s*), and lateral (*S*) columns of the cord.

Corresponding to each muscle segment two nerve roots arise from the cord, a dorsal root, with a ganglion (spinal ganglion) at some distance from the cord, and a ventral root, without a ganglion. The dorsal root contains only sensory fibres—*i.e.*, those carrying nervous impulses to the cord—and is afferent, while the ventral roots are efferent and contain only motor elements (Bell's Law). These roots unite into a mixed root, which then divides into dorsal and ventral branches.

The brain of vertebrates in general corresponds in its fundamental plan (fig. 568), best seen in development, with the brain of man. At an early stage it consists of three vesicles, one after the other, a fore brain (prosencephalon), a mid brain (mesencephalon), and a hind brain (metencephalon). Usually this stage is reached before the closure of the medullary folds. Formerly it was stated that a condition with five vesicles followed upon this with three, the mid brain remaining undivided, while the hind brain divides into cerebellum (*cb*) and medulla oblongata (*m*); the fore brain into cerebrum and 'twixt brain. This is unnatural so far as the hind brain is concerned, for cere-

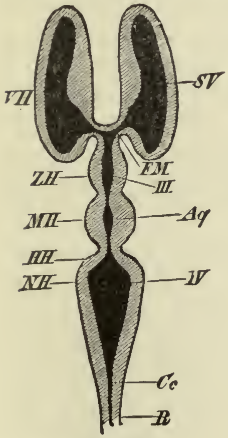


Fig. 568.

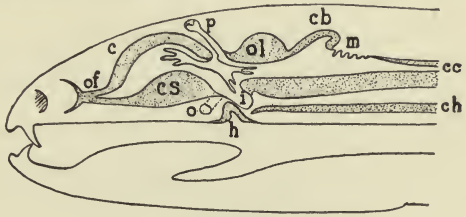


Fig. 569.

Fig. 568.—Diagram of a vertebrate brain. (From Wiedersheim.) *Aq*, aqueduct; *Cc*, central canal; *FM*, foramen of Monro (connexion of lateral ventricles with each other and with the third); *HH*, cerebellum; *MH*, corpora bigemina (optic lobes); *NH*, medulla oblongata; *R*, spinal cord; *SV*, lateral ventricles; *VH*, cerebrum; *ZH*, optic thalami ('twixt brain); *III*, *IV*, third and fourth ventricles.

Fig. 569.—Scheme of brain in sagittal section. *c*, cerebrum; *cb*, cerebellum; *cc*, canal of spinal cord; *ch*, notochord; *cs*, corpus striatum; *h*, hypophysis; *i*, infundibulum; *m*, medullary region; *o*, optic chiasma; *of*, olfactory lobe; *ol*, optic lobes; *p*, pinealis.

bellum and medulla are related to one another as roof and floor of one and the same cavity (fig. 569). The distinction between the first and second vesicles is problematical. The fore brain becomes divided into three parts by an inpushing at its anterior end: an unpaired middle portion, and in front a right and a left diverticulum. These paired portions, increasing in size, form the cerebral hemispheres, and together with a small connecting part represent the first cerebral vesicle, while the unpaired portion forms a second vesicle, the 'twixt brain.

Introducing the terms of human anatomy for the separate parts of the brain, the first vesicle consists of the two cerebral hemispheres whose dorsal and lateral walls are usually thick and are called the pallium, while in the floor of each hemisphere is an enlargement, the corpus striatum (*cs*). The spaces in the hemispheres are the first and second ventricles (*sv*). From the front portion of each hemisphere arises a distinct region, the olfactory lobe (*of*), which gives origin to the olfactory nerve. Since the organ of smell is frequently at some distance from the brain, the olfactory nerve must be elongate, as in the Amphibia (fig. 614), or the olfactory lobe must lengthen, as in many Elasmobranchs (fig. 592). In the latter case the swollen end of the lobe is close to the olfactory epithelium and is connected with the brain by a long stalk, the tractus, while the swelling is called the bulbus olfactorius. Both, as parts of the brain, must be distinguished from the olfactory nerve.

In the region of the second vesicle only the lateral walls become thickened, producing the optic thalami, directly adjoining the corpora striata; the roof of this vesicle develops no nervous substance, but remains a thin layer of epithelium closing in the third ventricle above (*III*). The floor is also thin-walled between the thalami and is pushed downwards, forming a funnel-like pocket, the infundibulum (*i*). The third vesicle, as a rule, is divided by a deep longitudinal dorsal groove, dividing the cavity into a right and left ventricle, while the two halves of the roof are known as the optic lobes or corpora bigemini. In the mammals alone (in which there is also a transverse groove dividing the optic lobes into the corpora quadrigemini) the cavity of this mid brain is reduced, by thickening of the walls, to a narrow canal, the iter or aqueduct of Sylvius, with the result that the term fourth ventricle is transferred to the cavity of the hind brain.

This last region is called the medulla oblongata; it is a prolongation of the spinal cord, and in many respects shows a similar structure. It is distinguished from the cord externally in that it gradually increases in size in front, while its roof is reduced to a thin epithelium, often torn away in dissection, leaving an opening, the fossa rhomboidalis, into the ventricle. In front of this fossa is the cerebellum, often a thin transverse nervous lamella, but usually is a considerable part of the brain, composed of a median 'vermis' and two lateral cerebellar hemispheres.

Although these five parts are present in all vertebrates, the appearance of the brain in the various classes is very different, because the relative size and form of the parts undergo great variations. In the lower vertebrates optic lobes and medulla oblongata are disproportionately large, while the cerebrum, and often the cerebellum, are insignificant in size; in the cerebrum, again, the hemispheres may be smaller than the corpora striata and the olfactory lobes. In the higher vertebrates, on the other hand, the cerebrum and cerebellum far surpass the other parts, the increase in size of the cerebrum being proportional to the increase in intelligence. The cerebral hemispheres grow backwards, in man and the apes covering the other parts, while in front the olfactory lobes are carried by a similar overgrowth to the lower surface. Since the capacity of the skull is limited, the cortex of the cerebrum, the seat of intelligence, is increased in amount by the development of folds, gyri, separated by sulci. Somewhat similar conditions exist in the cerebellum, which in mammals and birds is, next to the cerebrum, the largest part of the brain.

Connected with the 'twixt brain are two problematical organs, one, the epiphysis (pinealis), being dorsal; the other, the hypophysis (pituitary body), ventral. The hypophysis arises like a gland by an outgrowth from the embryonic mouth. This hypophysial pocket cuts off from its source, increases by budding, and fuses with parts derived from the end of the infundibulum to a single two-lobed body. It has been compared with the subneural gland of the Tunicata (p. 509). The epiphysis is an outgrowth from the roof of the brain, from which develops in many vertebrates the parietal organ. In many reptiles this has the structure of an eye (pineal eye), and in these, separated from the brain, but connected with it by a nerve, it lies in a special cavity in the parietal bone, which occurs not only in recent but in fossil forms. Above the eye the skin may be transparent.

The nerves which come from the brain mostly arise from the region between the mid brain and the spinal cord, especially from the medulla oblongata. The olfactory and optic nerves are an exception, the one arising from the cerebrum, the other from the 'twixt brain, but both, and especially the optic, differ so much from the peripheral nerves that they can hardly be classed with them.

Development shows that the optic nerve is a part of the brain. Following custom, however, and including these two, the pairs of cranial nerves may be enumerated in the terms of human anatomy as follows: I, N. olfactorius; II, N. opticus; III, N. oculomotorius; IV, N. trochlearis (patheticus); V, N. trigeminus; VI, N. abducens; VII, N. facialis; VIII, N. acusticus; IX, N. glossopharyngeus;

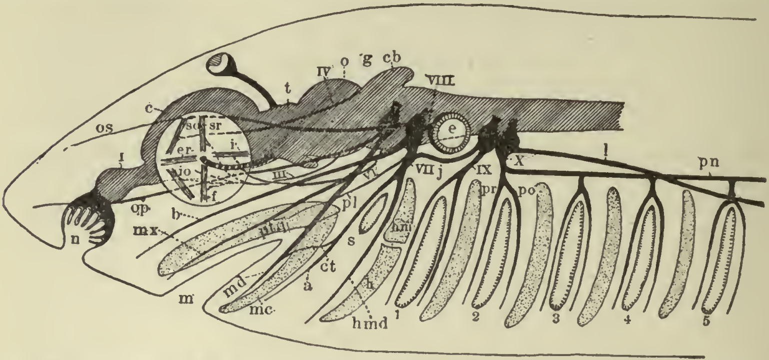


FIG. 570.—Diagram of cranial nerves (shark). *a*, alveolaris; *b*, buccalis; *c*, cerebrum; *cb*, cerebellum; *ct*, chorda tympani; *e*, ear; *er*, external rectus muscle; *f*, inferior rectus muscle; *g*, Gasserian ganglion; *h*, hyoid cartilage; *hm*, hyomandibular; *i*, internal rectus muscle; *io*, inferior oblique muscle; *j*, Jacobson's commissure; *l*, lateralis of vagus; *m*, mouth; *mc*, Meckel's cartilage; *md*, mandibularis; *mx*, maxillaris superior; *n*, nose; *o*, optic lobes; *op*, ophthalmicus profundus; *os*, ophthalmicus superficialis; *p*, pinealis; *pl*, palatine; *po*, posttrematic branches; *pr*, pretrematic branches; *pn*, pneumogastric (intestinal) of vagus; *ptg*, pterygoquadrate; *s*, spiracle; *so*, superior oblique muscle; *sr*, superior rectus muscle; *t*, 'twixt brain; *I–X*, cranial nerves; *1–5*, gill clefts.

X, N. vagus (pneumogastricus), XI, N. accessorius; XII, N. hypoglossus. The accessorius in fishes and amphibia is a part of the vagus; the hypoglossus, strictly speaking, belongs to the spinal nerves and only secondarily is associated with the cranial nerves, which explains its course, outside the skull, in cyclostomes and amphibia.

Since the head undoubtedly consists of several coalesced body segments (at least as many as there are visceral arches, and apparently more), the question arises whether the cranial nerves are as evidently segmental as are those of the trunk. To this is allied the further question whether Bell's Law that a mixed nerve consists of dorsal sensory, and ventral motor components is applicable here. Both problems have been much discussed in recent years, but as yet the final answers have not been given. It is probable that the present cranial nerves, the optic and olfactory excepted, have arisen by manifold rearrangements of segmental nerves. On the other hand it seems impossible to accept Bell's Law here without considerable modification, since many cranial nerves (facialis, trigemenus, etc.) contain motor fibres, although they are formed like dorsal roots.

Besides the nervous system of the body already outlined, the vertebrates have a special nervous system supplying the viscera,—the sympathetic system,—and in this a special central organ consisting of right and left cords beneath the vertebral column, in which ganglia are incorporated. The last of these ganglia lies at the base of the caudal vertebræ, the most anterior at the beginning of the neck. From the latter nerve cords extend into the head and are connected with ganglia (otic, sphenopalatine). This system sends out nerves in the form of delicate networks (plexus sympathetici) which usually accompany the blood-vessels to the vegetative organs (intestine, sexual apparatus, etc.). It is also connected with the spinal nerves.

Regarding the sense organs of the vertebrates we stand on firmer ground than with the invertebrates, since their great similarity to those of man supports the ideas of their functions derived from studies of their structure. The tactile organs make an exception, since only in land animals, and not in fishes, do they resemble those of man. These organs, in all forms above fishes, have the peculiarity that the nerves do not end in epithelial cells, but in special tactile cells of the derma, which either lie isolated in the connective tissue (Amphibia, reptiles), or, grouped together, produce tactile corpuscles (birds, mammals, fig. 571). These are oval bodies and are imbedded in special papillæ of the derma. In form and position they are much like the Vater-Pacinian corpuscles, which are distinguished by their histological structure (fig. 78) and, since they also occur in internal organs (mesentery of cat), are of problematic function. Besides these mesodermal nerve endings there are present in all vertebrates intraepithelial nerve branchings which are best seen in the cornea of the eye and in animals, like pigs and moles, with sensitive snouts. Even here the finest nerve twigs do not end in epithelial cells, but in small knobs between them.

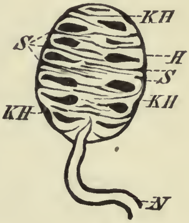


FIG. 571.—Tactile corpuscle from bird's tongue. *H*, outer envelope; *KH*, its nuclei; *N*, nerve; *S*, partitions.

Fishes lack tactile cells, tactile corpuscles, and end bulbs; hence the skin is provided with sense organs in which a sensory epithelium occurs. The dermal nerves pass into the epidermis and end in oval corpuscles, which, while imbedded in a stratified epithelium, consist of a single layer of sense cells. According to structure, nerve hillocks and nerve-end buds are distinguished. The first are the specific organs of the lateral line, to be mentioned later, of fishes and branchiate amphibians and amphibian larvæ, and therefore appear to subserve special and important sensations connected with aquatic life; hence the idea of a 'sixth sense,' lacking to man (*cf.* p. 125). The end buds are especially collected in the neighborhood of the mouth, on the lips and barbels. Since they also occur in the mucous membrane of the mouth, especially in the palatal regions, they connect with the taste organs. The taste buds have the same structure as the end buds of fishes. They occur in all classes of vertebrates, and are most abundant in man in the walls of the circumvallate papillæ at the base of the tongue; in rodents on the large foliate papillæ, etc.

The end buds also lead to the olfactory organs. The olfactory epithelium of many fishes and amphibia is a stratified epithelium with closely arranged end buds (fig. 572). By disappearance of the isolating parts of the ordinary epithelium the end buds form a continuous sensory epithelium, which is the rule in most vertebrates.

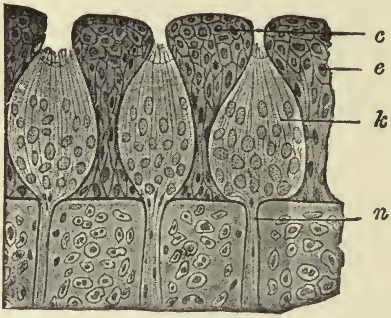


Fig. 572.—Section of olfactory epithelium of a fish (*Belone*). (From O. Hertwig, after Blaue.) *e*, epithelium; *k*, olfactory buds; *n*, nerves.

The olfactory organ, the nose, lined with its sensory epithelium, acquires a special interest both from its grade of development and from the important systematic distinctions it affords. Except the cyclostomes, which have an unpaired nasal sac, all vertebrates have paired olfactory organs. In adult fishes and in the embryos of higher forms are two pits which lie in front of or dorsal to the mouth; they are either distinct from it or only connected with it by an oronasal groove in the skin (fig. 599). If the animal be terrestrial and replace branchial by pulmonary respiration, a respiratory canal is developed in connexion with the nose. The oronasal groove closes to a tube which begins with an opening (nostril) on the surface and ends with a second opening (choana) in the mouth cavity. The olfactory sac proper is included in the wall of this tube, usually on its dorsal surface (fig. 573). In Amphibia, lizards, snakes, and birds the choana is far forward, behind the upper jaw; in alligators, turtles, and mammals it is carried far back, in crocodiles and some mammals (edentates) nearly to the vertebral column. This position is brought about by the development of the hard palate, a parting wall which divides the primitive mouth cavity into two portions, a lower, the persistent or secondary mouth cavity, and an upper, which, as secondary nasal cavity, contributes to the air passages. The bones of the maxillary and palatine series contribute to the hard palate, since premaxillaries, maxillaries, and rarely the pterygoids send out horizontal processes which meet in the middle line. In the mammals this partition is continued back by the muscular soft palate. In crocodiles there is a fibrous palate.

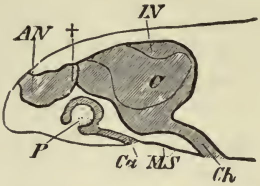


FIG. 573.—Diagram of nose of lizard. (After Wiedersheim.) *AN*, outer nasal cavity; *C*, olfactory sac; *Ca*, canal from Jacobson's organ to mouth; *Ch*, choana; *IN*, inner nasal cavity; *MS*, roof of mouth; *P*, Jacobson's organ; †, connexion between nasal cavities.

In the olfactory organ of the chordates two constituents must be recognized, an unpaired and two paired portions. The unpaired portion alone occurs in *Amphioxus*, this being supplied by the lobus olfactorius impar; in all vertebrates there are paired sacs with paired olfactory lobes. The unpaired sac of the cyclostomes has apparently arisen from a union of paired and unpaired parts, hence the double olfactorius.

A further increase in the nasal cavity is brought about by complicated folds in the walls supported by special skeletal parts, the turbinal bones, and also by the outgrowth of chambers, lined with mucous membrane which extends into the neighboring bones. Thus are formed the sinus frontalis in the frontal bone; behind, the sphenoid sinus in the sphenoid, and the antrum of Highmore in the maxillary. Again, a part of the primitive chamber lined with olfactory epithelium can be cut off from the rest and form an accessory nose, Jacobson's organ, which opens into the mouth behind the premaxillaries by 'Stenson's duct' (fig. 573, *P*). This organ is best developed in lizards, monotremes and ungulates, but often occurs in a reduced condition in other terrestrial vertebrates.

In all vertebrates with the exception of *Myxine* and a few forms living in the dark the eyes are composed of all the principal constituents which occur in the human eye and which have already been briefly described (p. 131, fig. 83). In most vertebrates it is a nearly spherical body with the optic nerve entering it from behind, with its interior occupied by transparent, refractive substances (lens, vitreous body), and its walls of three concentric layers. The outer of these is the tough protecting sclera (sclerotic), a usually fibrous, but in many fishes a cartilaginous, layer, which in front becomes transparent and strongly curved, forming the cornea. The second layer, the choroid coat, is richly vascular and pigmented; at the boundary between sclerotic and cornea it is changed to the iris. The inner layer is the retina, the structure and arrangement of which are characteristic of the vertebrates.

From the developmental standpoint the retina (fig. 82) consists of two parts, the retina proper and the tapetum nigrum (pigmented epithelium), formerly regarded as part of the choroid. In the retina the following layers are distinguished: (1) the limitans interna; (2) nerve-fibre layer; (3) ganglionic layer; (4) inner molecular layer; (5) inner granular layer; (6) outer molecular layer; (7) outer granular layer; (8) limitans externa; and (9) layer of rods and cones. The limitans externa is the bounding membrane of the embryonic retina, which is later penetrated by the rods and cones. Between the two limiting membranes Müller's fibres (*m*) extend, large supporting cells occurring in other sensory epithelia, the nuclei of which lie in the inner granular layer, and which are aided in their supporting function by the fine horny framework of both molecular layers. The nervous elements which are imbedded in this support are best understood by beginning with the optic nerve. This spreads out in the nerve-fibre layer, and on its way to the end apparatus comes twice into relation with ganglion cells; first in the ganglionic layer, second in the inner granular layer. Thus a great part of the retina (layers 1 to 6) are to be considered as an optic ganglion, such as occurs in molluscs and arthropods, but which there lies outside the sensory apparatus. The sensory epithelium (the retina in the sense this term is used in invertebrates) consists of but two layers, the outer granular layer and the rods and cones. The outer granules are the nuclei of the extremely slender epithelial cells which bear the rhabdomes (rods and cones) on their peripheral ends. Pigment cells are lacking between these visual cells, but the pigment so necessary for the visual function is supplied by the tapetum nigrum already mentioned. This is a layer of hexagonal epithelial cells which lies on the tips of the rhabdomes and sends pseudopodia-like processes between them, and since the tapetum is rich in black pigment granules, the rods and cones are enveloped in a close pigment mantle.

Although in this relation of pigment and in the union of the optic ganglion with the sensory cells important differences are to be noted from the eyes of the invertebrates, even of the closely similar cephalopod eye (p. 385), the most striking difference remains to be mentioned. The retina, with its limitans interna and nerve-fibre layer, abuts against the vitreous body; with its rhabdomes and tapetum against the choroid. Hence the incoming light must traverse the optic ganglion and pass through the layer of sense cells before reaching the end organs, the rhabdomes. In nearly all invertebrates, for example the Cephalopoda (fig. 383), the light falls directly on the peripheral end of the rhabdome. The rhabdomes in cephalopods, as in most invertebrates, are turned towards the light, in the vertebrates away from it.

This peculiar and functionally purposeless inversion of the vertebrate retina is explained by the development of the eye. This can be divided, according to origin, into two parts, a cerebral (optic nerve, retina, tapetum) and a peripheral (all other parts). As the eye in tunicates and *Amphioxus* is permanently a part of the brain, so is the retina of vertebrates genetically, and of the first cerebral vesicle. An outgrowth occurs on either side (fig. 574, *B*) of the 'twixt brain and becomes expanded distally to an optic vesicle which is connected with the brain by an optic stalk. The vesicle extends out to the periphery and, coincidently with the development of the lens, is folded into a double-walled optic cup with outer or tapetal, inner or retinal layers. If the position of the epithelial cells be followed, it will be seen that the peripheral ends rest upon the tapetum, and when these ends develop the rhabdomes, these must grow into the tapetal layer.

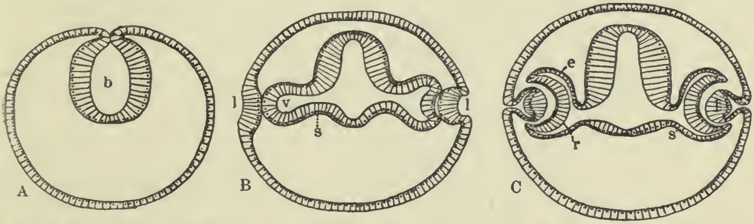


FIG. 574.—Diagram showing the inversion of layers in the formation of the retina (orig.). The nuclei are placed in the (morphologically) deeper ends of the cells. In *A* the brain (*b*) has been closed in ; in *B* the optic vesicle (*v*) has reached the lens (*l*) and on the right is being converted into the double-walled optic cup with, as shown in *C*, an outer tapetal (*e*) and an inner retinal layer (*r*).

In contrast to the retina, the lens develops as an invagination from the epithelium of the body (fig. 574) ; sclera, cornea and vitreous body from connective tissue. Thus the important part of the eye arises from the brain and is later provided with accessory apparatus which arise from peripheral parts. The invertebrate eye, on the other hand, with all its parts arises from the skin.

The vertebrate eye is furnished with secondary structures: with muscles which move it, with lids which protect the cornea from injury and drying. The lids are dermal folds which extend over the eyeball from above and below. To these a third lid, the nictitating membrane, may be added. It arises from the inner angle of the eye, and can extend over the cornea beneath the upper and lower lids. A special lachrymal gland, which occurs at the outer angle of the eye, provides the fluid to moisten the cornea, while a second or Harder's gland occurs at the inner angle when a nictitating membrane is present. Both are lacking in the Anamnia.

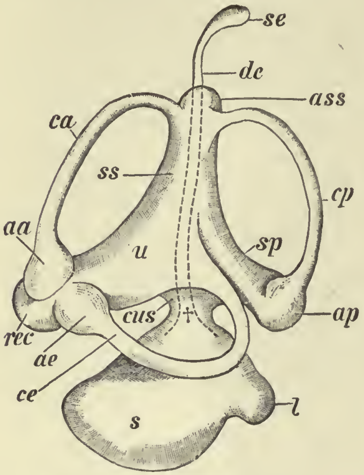


FIG. 575.—Diagram of membranous labyrinth of a fish. (From Wiedersheim.) *aa*, *ae*, *ap*, anterior, external, and posterior ampullæ; *ass*, superior utricular sinus; *ca*, *ce*, *cp*, anterior, external, and posterior semicircular canals; *cus*, utriculosaccular canal; *de*, ductus endolymphaticus; *l*, lagena; *rec*, recessus utriculi; *se*, sacculus utriculi; *ss*, superior utricular sinus; *sp*, posterior utricular sinus; *u*, utriculus; †, origin of endolymph duct.

The ear, at the level of the medulla oblongata, rivals the eye in its complication of structure. In development it has one point in common with the invertebrate otocyst—it arises as an ectodermal pit which is usually completely cut off from its parent layer, and only in elasmobranchs remains connected with the exterior by a tube, the elsewhere closed endolymphatic duct. In the cyclostomes it consists of a single vesicle with a single macula acustica; from the fishes upwards the vesicle becomes divided by a constriction into an upper utriculus and a lower sacculus (fig. 575), the connecting utriculosaccular duct being narrow in the mammals. Both utriculus and sacculus receive a part of the macula acustica. Diverticula from the vesicle occur, giving the whole the name of labyrinth. From the utriculus arise three semicircular canals, connected at either end with this cavity, each swollen at one end to an ampulla, containing a special nerve termination, the crista acustica. These canals stand at right angles to each other in the three dimensions of space and without doubt subserve the sensation of equilibration (p. 128). They are an outer horizontal, an anterior vertical (nearly sagittal), and a posterior vertical (nearly transverse). The non-ampullar ends of the two vertical canals unite, a condition which is understood when it is recalled that in cyclostomes these canals alone are present, and in *Myxine* form a single canal with two ampullæ. A later formation is a diverticulum from the sacculus, which appears even in the fishes as a small pocket, the lagena, containing a part of the macula acustica; in the reptiles and birds the lagena becomes much larger, and in the mammals is spirally coiled and is known as the cochlea. A part of the macula acustica of the lagena develops into a special nerve-end apparatus, the organ of Corti.

The membranous labyrinth described above is partially or entirely enclosed in the side wall of the skull in the otic capsule, which may ossify to the otic or petrosal bones. In the birds and mammals the enclosure is such that the structure is duplicated in bone, so that the membranous labyrinth lies in a bony labyrinth, the two being separated by lymph spaces (fig. 576). These spaces are developed in the cochlea into two tubes, the scala tympani and scala vestibuli, the two connecting only at the tip, being separated elsewhere in part by the membranous cochlea (the ductus cochlearis or scala media). The spaces of the bony labyrinth are filled by two different fluids: inside the membranous labyrinth an endolymph, and between this and the walls of the bony labyrinth a perilymph.

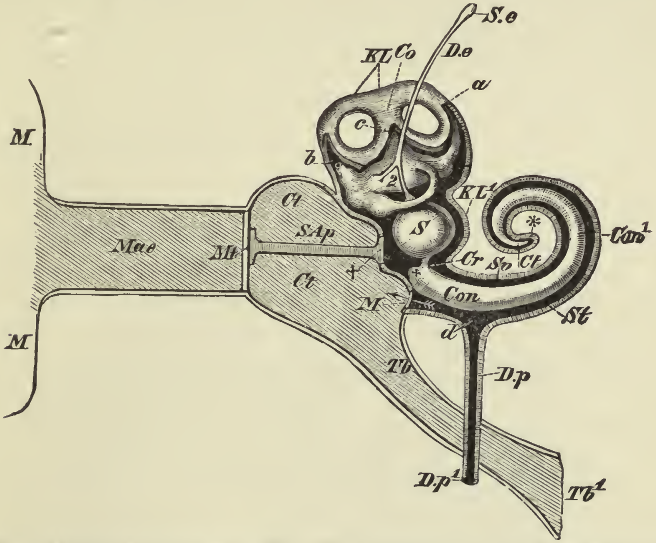


FIG. 576.—Diagram of human ear. (From Wiedersheim.) *a*, *b*, vertical semicircular canals; *c*, their upper connexion; *Co*, the connexion in bony labyrinth; *Con*, ductus cochlearis; *Con′*, cochlea; *Cr*, canalis reuniens; *Ct*, tympanic cavity (left), cupula terminales (right); *d*, perilymph; *De* ductus endolymphaticus; *Dp*, *Dp′*, ductus perilymphaticus; *Kl*, *Kl′*, bony labyrinth surrounding the membranous labyrinth, the perilymph space black; *M*, conch of ear (left), membrane closing fenestra rotunda (right); *Mae*, external auditory meatus; *Mt*, tympanic membrane; *S*, sacculus; *SAp*, ear bones (represented as a rod); *Se*, sacculus endolymphaticus; *St*, *Sv*, scalæ tympani and vestibuli; *Tb*, *Tb′*, Eustachian tube and its entrance into pharynx; *, connexion between scalæ tympani and vestibuli; †, insertion of ear bones in fenestra ovalis; *2*, utriculus.

Accessory structures may be added to this auditory apparatus proper, their purpose being to bring sound waves to it. Such structures are but occasionally present in fishes (it is not certain that they hear), since the sound waves are easily carried by the water to the tissues and thence directly to the ears. On the other hand, with the change to terrestrial life such a sound-conducting apparatus is necessary on account of the differing densities of the air and the tissues. So we find from Amphibia onwards a vibrating membrane—the tympanic membrane—which receives the sound vibrations from the air and carries them to a chain of ear bones (ossicula auditus), which in turn transmits them to the inner ear or labyrinth. These structures are not always functional (cetacea), and they may be wholly or in part rudimentary (urodeles, snakes, Amphisbænids).

To understand this apparatus it must be recalled that the ear lies between the hyoid and mandibular arches in the neighborhood of a canal which leads from the surface to the pharynx. In the fishes this canal is the spiracle, a reduced gill cleft. In the Anura and amniotes it consists of an air chamber closed externally by the tympanic membrane, stretched on a tympanic annulus, while the opening to the pharynx is retained. The part next the membrane becomes expanded into the tympanic cavity, this with the membrane forming the tympanum or drum. The part connecting with the pharynx is usually narrowed and is called the Eustachian tube. The membranous labyrinth lies in the wall of the tympanic cavity and touches it at one or two points where the bony auditory capsule is interrupted, the always present fenestra ovalis, and the fenestra rotunda, lacking in Amphibia.

When it is recalled that the mandibular arch lies just in front of the spiracle, and the hyoid close behind it, it is readily understood how parts of these arches can enter the tympanum and produce the ear bones. In Anura, reptiles, and birds a columella has one end attached to the stapedial plate, which lies in the fenestra ovalis, while the other is inserted in the drum membrane, the whole conveying the waves across the tympanum to the labyrinth. In the mammals the structure is different, since the columella is replaced by two bones, the malleus, which is attached to the drum membrane, and the incus, which articulates with the

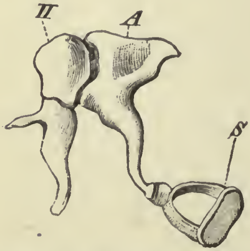


FIG. 577.—Ear bones of man. (From Wiedersheim.) *A*, incus; *II*, malleus; *S*, stapes.

stapes. Most students believe incus and malleus to be parts (quadrate and articulare) of the mandibular arch—a view which has its opponents, who believe these to be a divided columella (fig. 577).

The tympanic membrane is usually flush with the surrounding skin or only slightly below its level. In the mammals it is protected by being placed at the bottom of a deep tube, the external auditory meatus. The ear conch, a fold of skin supported by cartilage, is also confined to the mammals.

The more important vegetative organs of the body are enclosed in a large body cavity or cœlom beneath the vertebral column. This is, as development shows, an outgrowth from the primitive digestive tract, an enterocœle (pp. 109 and 158), lined with epithelium. Since it arises, as in other cœlomate animals, by paired outgrowths from the archenteron, it follows that at first the two cavities must be separated by a partition which also encloses the intestinal tract (fig. 578). These walls furnish the mesentery which supports the intestine in its

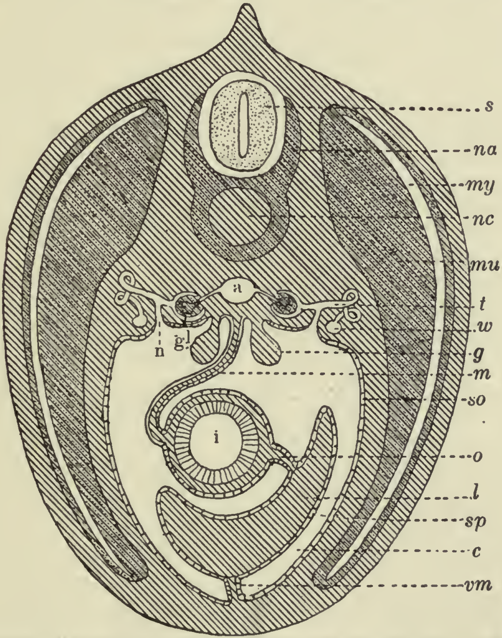


FIG. 578.—Section of vertebrate in abdominal region. (From Kingsley.) *a*, dorsal aorta; *c*, cœlom; *g*, gonad; *gl*, glomerulus; *i*, digestive tract; *l*, liver; *m*, mesentery; *mu*, muscular part of myotomes; *my*, its cœlom (myocœle); *o*, omentum; *s*, spinal cord; *so*, *sp*, somatic and splanchnic epithelia; *t*, nephridial tubule; *vm*, ventral mesentery; *w*, Wolffian duct.

whole length from the vertebral column, but ventral of the digestive tract (as the mediastinum, omentum minus, and suspensory ligament of the liver of human anatomy) only reaches as far back as the liver, so that right and left cœloms unite behind. Some other organs are also suspended in the body cavity by membranes: the testes by the mesorchium, the ovary by the mesovarium.

The body cavity is frequently called the pleuroperitoneal cavity, since in mammals it is divided by a partition, the diaphragm, into an anterior or pleural and a posterior or peritoneal (abdominal) cavity. The lining membranes of these cavities are called pleura and peritoneum respectively. The pericardial cavity is also a derivative of the cœlom, and the lining, the pericardium, but a part of the pleuroperitoneal membrane. Hence it is that in many fishes (sharks, sturgeon) a communication persists between the pericardial and the other cœlom. In most fishes and in many reptiles there is a direct connexion of the cœlom with the exterior by one or two pori abdominales, beside or behind the anus.

The alimentary tract possesses the greatest systematic interest of the vegetative organs, for it not only is concerned with digestion, but furnishes, as in all chordates, the respiratory organs (gills and lungs) as well, these arising in the non-chordates from the ectoderm. It begins with the anterior ventral mouth and ends ventrally with the anus, some distance in front of the tip of the tail; it is almost wholly entodermal in origin, there being but slight ectodermal portions at either end.

The first division is spacious and consists of the ectodermal mouth cavity and the entodermal pharynx, two spaces which, in most vertebrates, are not sharply marked off, but in alligators and mammals are separated by the soft palate. Then begins the narrow œsophagus, widening behind to the stomach. From the hinder or pyloric end of the stomach begins the small intestine, which enlarges into the large intestine, separated from the small intestine in the higher vertebrates by a valve and one or two cæca. The terminal portion in most vertebrates is called the cloaca because it receives the urogenital ducts. The liver is the only gland constantly present; it is a large compact brown organ, generally provided with a gall bladder. Usually a smaller gland, the pancreas, occurs. The ducts of the liver (bile duct, ductus choledochus) and pancreas empty into the small intestine near the pylorus. The mouth cavity may have salivary glands connected with it, while the rectal region occasionally has blind sacs and glands.

A striking vertebrate characteristic occurs in the dentition. In the cyclostomes there are horny teeth—strongly cornified epithelial products seated on connective-tissue papillæ; in the higher groups occur true teeth of dentine and enamel, enclosing a richly vascular pulp. They occur in places where the underlying skeleton affords them a firm support, especially on the upper or lower jaws, but they may occur on other bones of the mouth and pharyngeal cavities (roof of the mouth, gill arches). They have apparently arisen from a diffuse dentition, recalling the scales of the skin, since many elasmobranchs possess, besides the ordinary teeth, rudimentary teeth in mouth and pharynx. Where teeth are lacking (birds, turtles, baleen whales) they have been lost.

The respiratory organs arise from the pharynx. In the fishes and some Amphibia its walls, right and left, are perforated by gill clefts, each of which lies between two successive visceral arches (fig. 570). These are canals which open internally into the pharynx, while the outer gill openings are on the outer surface. The anterior and posterior walls of the clefts bear delicate vascular folds of mucous membrane, the gill filaments. These are the internal gills, in contrast to the external gills of Amphibian larvæ, which are dendritic external ectodermal growths arising above and between the gill slits (figs. 4, 5). It is important for the phylogeny of the vertebrates to note that reptiles, birds, and mammals, which never breathe by gills, have gill clefts outlined and later lost with the exception of the Eustachian cleft.

Two problematical organs, the thymus and the lateral lobes of the thyroid gland, develop from the epithelium of the gill clefts. The middle unpaired part of the thyroid has been regarded as a modification of the endostyle of the Tunicata (p. 506). The thyroid, which produces iodine compounds, is doubtless very important; disease or extirpation of it causes serious nervous disturbances.

The lungs also arise from the pharynx as two sacs (one occasionally remaining rudimentary), which grow downwards and backwards. They retain their opening into it either directly or by means of a trachea or windpipe, which just before its entrance into the lungs usually divides into two bronchi (figs. 579, 620). At the opening into the pharynx (glottis) the supporting cartilages (remnants of the visceral skeleton, p. 524) are strong and form the larynx, which in mammals may be closed from the pharynx by a valve, the epiglottis. The lungs and trachea have their counterparts in the fishes in the swim bladder, a hydrostatic apparatus, and its duct.

The swim bladder of fishes and the lungs of most amphibia are smooth-walled sacs, but in some have greater respiratory surface since folds extend into the central space. This peripheral folding increases in the reptiles at the expense of the central chamber, this in some being completely divided by the partitions, which extend inwards from the walls to the bronchus. In the mammals a central chamber is lacking; the bronchi extend into the lungs, branching again and again to the fine bronchioles which give off alveolar ducts lined with minute air cells or alveoli.

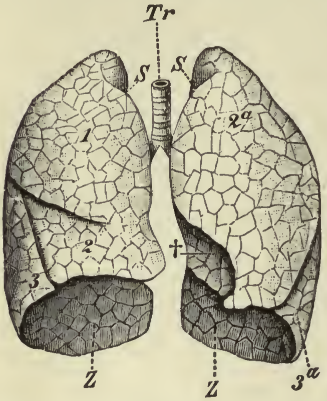


FIG. 579.—Lungs of man, ventral view. (From Wiedersheim.) *S*, sulcus for subclavian artery; *Tr*, trachea dividing below into the two bronchi; *Z*, position of diaphragm; *1*, *2*, *3*, *2a*, *3a*, lobes of right and left lungs.

The circulatory apparatus is easily derived from that of annelids, and, like it, is completely closed. In the annelids (p. 307, figs. 272, 275, 276) above and below the digestive tract is a longitudinal blood-vessel, these being connected in each somite by loops which pass around the intestine. The vertebrate scheme varies in the development of a heart in the ventral trunk (the dorsal of the annelid). In the lower vertebrates, the fishes (figs. 65, 597), the heart lies close behind the gills and sends to them the blood which it receives from the body. Hence, like the whole ventral trunk, it carries venous blood. Since the anterior loops, the gill arteries, pass through the gills, the dorsal trunk, which collects from these, must contain oxygenated blood, which is sent by the carotids to the head, and by the dorsal aorta and the vascular loops to the body. It thus becomes venous and flows back into the ventral trunk.

This scheme of circulation in fishes needs further description. The heart, a strong muscular organ enclosed in a pericardium, consists of two parts, auricle and ventricle, separated by valves. The trunk (ventral aorta) arising from the auricle is arterial and corresponds to the ascending aorta and pulmonary artery of man. The arterial arches of the gill region which arise from it pass directly into the dorsal vessel only in young fishes (fig. 597); later they furnish the branchial circulation of gill arteries, gill capillaries, and gill veins (fig. 65). The dorsal trunk is the dorsal aorta (aorta descendens); the ventral trunk, which only occurs in the embryo, is the subintestinal vein, from which the portal vein arises. To this are added a system of paired veins, consisting of Cuvierian ducts and jugular and cardinal veins, the latter with growth encroaching more and more into the territory of the subintestinal vein.

The circulation of the fish type undergoes a great modification with the loss of gills and the appearance of pulmonary respiration. Gills and gill capillaries disappear, and the branchial circulation is reduced to arterial arches leading direct from the ventral to the dorsal aorta. The swim bladder received its blood from the body (systemic) circulation, but with the functioning of the lungs pulmonary arteries and veins come into existence, while the arterial arches in part disappear, in part are divided between the pulmonary and systemic circulations (fig. 580). Of the six arches which usually appear in the embryo, the first and second, and the fifth in animals with lungs, usually disappear. The last arch (*4*), which even in the Dipnoi supplies the swim bladder, becomes a pulmonary artery, the other arches (*1* and *2*) furnish the systemic portions, the dorsal aorta (*2*) and the carotids supplying the head (*1*). Since special pulmonary veins, distinct from the systemic circulation, carry the blood from the lungs to the heart, the heart becomes divided by a septum which separates it into right and left halves. The right half retains the venous character of the fish heart; since the right auricle receives the systemic veins, the right ventricle gives off the pulmonary artery. The left half is purely arterial, receiving arterial blood by the left auricle from the lungs and sending it out through the aorta ascendens to the body. A complete separation of pulmonary and systemic circulation, and a corresponding division of the heart, occurs only in birds and mam-

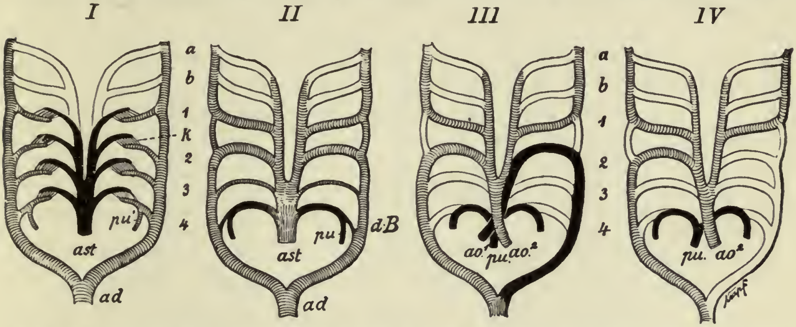


FIG. 580.—Diagram of modification of arterial arches in various vertebrate classes. White, vessels which degenerate; cross-lined, vessels containing arterial blood; black, vessels containing venous blood. *I*, Dipnoi; *II*, Urodeles with pulmonary respiration; *III*, Reptiles; *IV*, Birds (in mammals the left instead of the right aortic arch persists). ao^1, venous aorta of reptiles; ao^2, arterial aorta; *ast*, arterial trunk; *a*, *b*, arches which usually disappear; *ad*, dorsal aorta; *d.B*, ductus Botalli; *k*, gill capillaries; *pu*, pulmonary artery; *1–4*, persistent arterial arches.

mals. Reptiles and amphibia show how the modification has been accomplished. In these the separation begins in the venous system and extends to the auricle, in the reptiles the septum arises in the ventricle. In the arterial system remnants may persist, such as a connexion (ductus Botalli) of the pulmonalis with the aorta (*II, d.B*), or an aortic arch may arise with the pulmonalis from the right side of the heart (*III, ao*).

Besides blood-vessels, lymph vessels occur in the vertebrates as complements of the venous system. The fluids which collect in the spaces of the connective tissue are taken by them and carried into the large venous trunks. Usually the action of the heart and the movements of the body are sufficient to cause the flow of this lymph, but special lymph hearts may occur. The lymph vessels distributed to the digestive tract play an important rôle, since they serve in the resorbtion of digested food. They are called chyle ducts because their contents, the chyle, rendered white by oil globules at the time of digestion, distinguishes them from other lymphatics. The most important features of lymph and blood have already been noticed (p. 88). In special places small bodies, the lymph glands, are inserted in the course of the lymph vessels, in which lymph corpuscles arise. Among these from its structure is to be enumerated the spleen, colored bright red by its rich blood supply.

The sexual and excretory organs are so closely associated that they are generally united as the urogenital system. The sexual products are formed in the embryo from a special region of the peritoneal epithelium on either side of the vertebral column. These primordial cells early leave their primitive position, and sink into the underlying connective tissue (fig. 33), forming in the male glandular tubes, in the female cords which break up into numbers of round follicles, each containing a single larger cell, the ovum. In the male the gonads thus formed are compact and frequently oval, the testes; in the female they are looser and follicular ovaries.

The deposition of the sexual cells occurs in many fishes by way of the body cavity and the abdominal pores, and in this case a part of the cœlom may be cut off as a special vas deferens or oviduct. In most vertebrates the ducts are formed from a part of the nephridial system. Embryology shows that there are three kinds of nephridia in vertebrates: (1) the pronephros, or head kidney; (2) mesonephros, or Wolffian body; (3) metanephros, or kidney proper, with the corresponding pronephric, mesonephric (Wolffian), and metanephric (ureter) ducts. The first two of these ducts are genetically connected, since the development of the elasmobranchs shows that the pronephric duct, by splitting, gives rise to two canals, the Wolffian (mesonephric), and the Müllerian ducts, the latter retaining its relation to the pronephros.

The pronephros is usually functional only in embryonic life and then only in early stages, possibly in some cases not at all. Its relations to the other parts are yet in question. In most

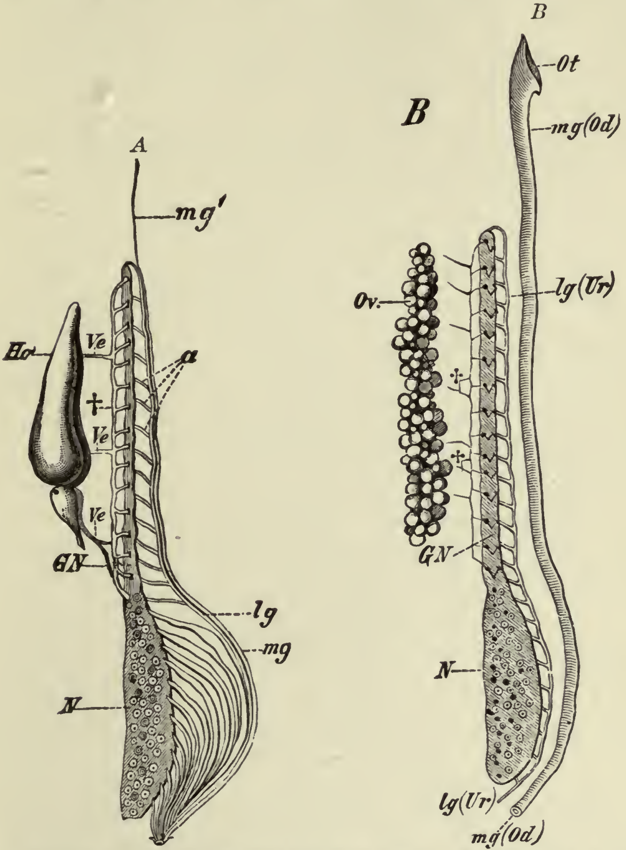


Fig. 581.—Scheme of urodele urogenital system based on *Triton*. (From Wiedersheim, after Spengel.) *A*, male; *B*, female. *a*, excretory ducts; *gn*, sexual part of mesonephros; *Ho*, testis; *lg*, Leydig's duct (ureter); *mg*, Müllerian duct (oviduct); *mg′*, its vestigial end in male; *N*, functional part of mesonephros; *Ov*, ovary; *Ot*, ostium tubæ; *Ve*, vasa efferentia; *, collecting duct of vasa efferentia (rudimentary in *B*).

teleosts the mesonephros is equally developed in nearly the whole length of the body cavity, but in the Amphibia (fig. 581) and many elasmobranchs its anterior part is smaller than the rest, a condition which has its explanation in its relations to the sexual apparatus.

In the males (excepting many fishes) the testes become connected with the anterior end of the Wolffian body (fig. 581, *A*), so that the urinary tubules of the latter come to be seminal ducts, while the hinder portion remains excretory, this condition being permanent in the Amphibia. In the amniotes the anterior mesonephros retains its connexion with the testes, forming the vasa efferentia, while the Wolffian duct forms the vas deferens, a portion of it greatly coiled being the epididymis. The remainder of the Wolffian body degenerates, a portion only persisting as the paradidymis.

In the females (fig. 581, *B*) the mesonephros is smaller in front, as in the males, but the connexion of this with the ovary does not exist, so here the Wolffian duct is solely excretory, and not, as in the males, excretory and seminal duct. In the female amniotes the Wolffian body almost entirely disappears, for in both sexes of the reptiles, birds, and mammals the metanephros or kidney proper is a new formation, growing forwards from the posterior end of the Wolffian duct. In the females of elasmobranchs, Amphibia, and Amniotes the Müllerian duct serves as an oviduct, its anterior end opening by the ostium tubæ into the abdominal cavity and receiving the eggs as they escape from the ovary. In the male the Müllerian duct disappears early.

The union of sexual and excretory organs to a urogenital system arises from the same relations as in the annelids; both organs arise from the cœlomic epithelium and have temporary or permanent connexion with the body cavity. This has already been described for the gonads. The urinary tubules of both pro- and mesonephros are derivatives of the cœlomic epithelium and possess an arrangement recalling that of the annelids in a striking manner. As is shown (fig. 70) in the scheme of the embryo selachian, the nephridial system consists of numerous canals, segmentally arranged, connected by funnels (nephrostomes) with the body cavity; and differs from the segmental organs of the annelids in that they do not open singly to the exterior, but by a common duct. They also differ in their further development by increasing greatly in number and forming a compact organ, and, finally, by the formation in a certain part of a network of blood-vessels, the glomerulus, which pushes into the lumen of the tube.

The ducts of the urogenital system open behind the anus in most fishes on a urogenital papilla; in the elasmobranchs, amphibians, birds, and most reptiles dorsally into the hinder part of the digestive tract, which thus becomes a cloaca. In turtles and mammals the urogenital canal opens into the urinary bladder, a ventral diverticulum of the rectum which first appears in the

Amphibia. Urinary and sexual ducts then either open into the urogenital sinus, the lowest part of the bladder leading to the cloaca (turtles, monotremes), or this part receives only the genital ducts, while the ureters enter the base of the bladder. The urogenital sinus remains in connexion with the cloaca in the turtles and monotremes; in the other mammals a cloaca occurs only in embryonic life. Later, by formation of the perineum, the cloaca is divided into a hinder digestive and an anterior urogenital canal. Step by step the stages may be followed from urogenital ducts opening behind to those opening in front of the anus.

Asexual and parthenogenetic reproduction are unknown in the vertebrates. The impregnation of the eggs in the lower groups is usually external and occurs during oviposition; in the higher internal copulation is effected by opposition of the genital orifices or by the development of an intromittent organ, the penis. The fertilized egg can undergo a part or the whole of its development in specialized parts of the oviduct (uterus). Accordingly viviparous and oviparous forms are distinguished, and between these extremes those that are ovoviviparous (*cf.* p. 161). Most elasmobranchs are viviparous, but many are oviparous. In the teleosts oviparous forms predominate, but there are viviparous exceptions. So, too, among the reptiles and Amphibia there are some viviparous species among the egg-laying majority. The birds and mammals are most constant, the first being exclusively ovoviviparous, while all the mammals bring forth living young with the exception of the ovoviviparous monotremes.

Three embryonal appendages may occur in the development, the yolk sac, the amnion, and the allantois. The yolk sac is small in those vertebrates which have some yolk, but not enough to cause meroblastic segmentation (Amphibia), yet it is everywhere present and is best developed in those groups (fishes, fig. 582, reptiles and birds) with discoidal segmentation, and is the result of the accumulation of food material in the digestive tract, which forces out its ventral wall like a hernia. Its presence in the mammals, which have small eggs lacking in yolk, is an indication that these have descended from large-yolked forms, such as the monotremes yet are. The embryo either lies directly on the yolk or is connected with it by a yolk stalk.

While the yolk sac is widely distributed, the amnion and allantois are restricted to reptiles, birds, and mammals, which are consequently spoken of as Amniota or Allantoidea, in contrast to the fishes and Amphibia, which are frequently called Anamnia or Anallantoidea, from the absence of these structures. The amnion is a sac which envelops the whole embryo and is connected with the rest only at the umbilicus, that is, the point where the yolk sac projects from the ventral wall. In this sac is an albuminous amniotic fluid. The amnion is genetically a part of the ventral surface; it develops ventrally as folds—lateral, anterior, and posterior—which grow up over the back on all sides and unite above the embryo.

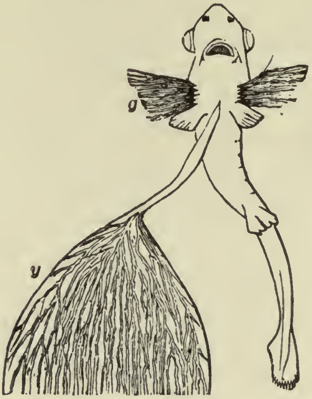


FIG. 582.

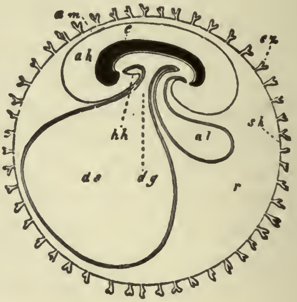


FIG. 583.

FIG. 582.—Shark embryo. (From Boas.) *y*, part of yolk sac ; *g*, external gills in front of pectoral fins.

FIG. 583.—Embryonic envelopes of a mammal. (Diagram after Kölliker.) *ah*, amniotic cavity ; *al*, allantois ; *am*, amnion ; *dg*, yolk stalk ; *ds*, yolk sac ; *e*, embryo ; *hh*, ventral wall of embryo; *r*, extra-embryonic cœlom; *sh*, serosa ; *sz*, serosal villi.

The allantois is an enlargement of the urinary bladder. This grows out from the body cavity at the umbilicus and extends between yolk sac and amnion and then grows in all directions until its folds meet above the back. The part of the allantois which receives the urine may be enlarged or not. The rest of the outgrowth consists of blood-vessels and connective tissue. The blood-vessels are the most important, for the allantois forms the respiratory apparatus of the embryo, and in the mammals it develops the placenta, by which nourishment as well is conveyed to the young. Yolk sac, amnion, and allantois are enveloped in a common coat, the serosa.

Aristotle and his followers recognized four divisions of vertebrates, and these were retained by Linné and Cuvier under the names Pisces, Reptilia or Amphibia, Aves, and Mammalia. Blainville (1818) divided the second of these into two classes, retaining the name Reptilia for the one, Amphibia for the other. Milne Edwards showed that this division corresponded with one between the higher and lower groups, the amniote and the anamniote divisions. Later Haeckel divided the fishes, separating the Cyclostomes from the others as a distinct class, while Huxley pointed out the close resemblances between the reptiles and birds, grouping them as Sauropsida. Another division of convenience but not of much systematic importance contrasts the fishes with all other forms, the Tetrapoda, so called from the possession of legs rather than fins.

SERIES I. ICHTHYOPSIDA (ANAMNIA, ANALLANTOIDA).

Vertebrates respiring for a time or throughout life by means of gills; neither amnion nor allantois present in the embryo.

Class I. Cyclostomata (Marsipobranchii, Agnatha).

The class of Cyclostomes contains but few species, among which the lamprey eels and the slime or hag fishes are best known. In shape they are eel-like. They are distinctly vertebrate in the possession of large liver and nephridia; of a muscular heart with auricle and ventricle, lying in a pericardium; olfactory lobes, epiphysis and hypophysis, and the higher sense organs. In the brain, cerebrum and cerebellum are not so prominent as are the optic lobes and medulla. The inner ear is not divided into utriculus and sacculus, and it has but one or two semicircular canals, but always two ampullæ. The skin (fig. 26) consists of derma and a stratified epidermis.

The cyclostomes are distinguished from the true fishes by the lack of a vertebral column. The axial skeleton of the trunk consists either of the notochord alone or of it and small neural arches. A cranium and a basket-like gill skeleton are present, but so different are these from those of other vertebrates that homologies are difficult. The absence of paired fins is important. Since the median fins are supported by horny threads alone, the cartilaginous appendicular skeleton—alone of importance—is entirely wanting. Then the skin lacks scales, and the mouth true dentine teeth, for the pointed brown teeth arranged in circles in the mouth of the lamprey (fig. 584), and the fewer teeth of the myxinoids, are purely epidermal products and cannot be compared with the teeth of other vertebrates. Other important differences have given rise to names applied to the group.

The name Cyclostomata refers to the circular mouth, an external feature, which, however, rests on the important fact that the jaws are absent or extremely rudimentary, and do not close on each other as do the jaws of other vertebrates. This cyclostome condition is of value to the animals, as it aids them in sucking on to other animals. At the base of the dome-like mouth cavity is the so-called tongue, which is the sucking apparatus, since it can be drawn backwards like a piston (fig. 584).

The name Marsipobranchs has been given on account of the form of the gills, which are usually six or seven in number, but in *Bdellostoma* may be twelve or fourteen on either side. Each gill cleft consists of three parts, the gill sac (marsupium), which alone contains gills, and the afferent and efferent ducts (fig. 585). These canals arise separately, and may continue so (*Bdellostoma*), but in *Petromyzon* the afferent ducts unite to a single tube which opens ventrally in the pharynx. In *Myxine* (fig. 585) the conditions are reversed, the efferent canals uniting to empty through a single external opening.

A third name, Monorhina, has been given, since these forms, in contrast to all other vertebrates, have an unpaired olfactory organ. The single nostril, lying in the mid line of the head, opens into a nasal sac, from the bottom of which a canal descends towards the roof of the mouth, ending blindly in Petromyzontes (Hyperoartia), or penetrating it in the Myzontes (Hyperotretia), so that an inner nasal opening (choana) occurs. A paired olfactory nerve supplies the organ.

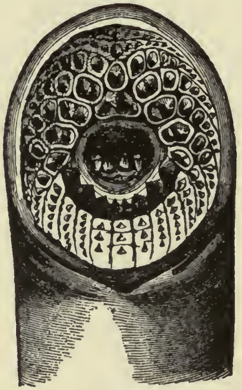


FIG. 584.

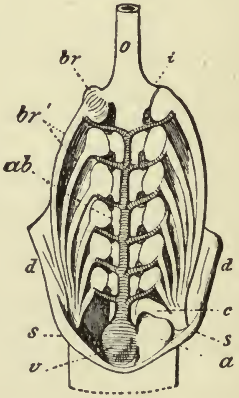


FIG. 585.

FIG. 584.—Mouth of *Petromyzon marinus* with horny teeth and tongue. (From Gegenbaur.)
FIG. 585.—Gill apparatus of *Myxine glutinosa*. (After J. Müller.) *a*, atrium; *ab*, gill artery and gill arch: *br*, gill sac (the lines show the gills); *br'*, efferent canal; *c*, œsophageo-cutaneus duct; *d*, skin turned away; *i*, afferent gill canal; *o*, œsophagus; *s*, mouth of atrium; *v*, ventricle of heart.

Sub Class I. Myzontes (*Hyperotretia*).

Semiparasitic cyclostomes with cirri around the mouth, very primitive nephridia, right and left rows of slime sacs, eyes rudimentary (lens, sclera, and choroid lacking). From the large amount of mucus they are known as slime eels. They bore into fishes and eat the flesh. *Myxine** on the east coast, *Bdellostoma** (*Polistotrema*) on the west.

Sub Class II. Petromyzontes (*Hyperoartia*).

Several American species of lampreys, all belonging to *Petromyzon** (with sub genera), have well-developed dorsal fins, and seven branchial openings. They occur in salt and fresh water, some marine species ascending streams to lay their eggs. The young pass through a larval (Ammocœtes) stage with rudimentary eyes and slit-like mouth. Many of the species live on the mucus and blood which they rasp from fishes.

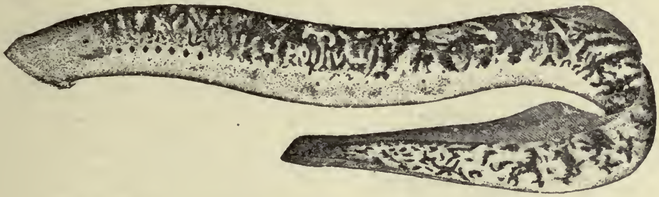


FIG. 586.—*Petromyzon marinus*,* sea lamprey. (After Goode.)

Here may be mentioned a group of fossils, the OSTRACODERMI, of uncertain position. They have fish-like bodies, but no skeleton or jaws are known. They flourished in paleozoic seas. *Pteraspis*, *Cephalaspis*, *Pterichthys*.

Class II. Pisces (Fishes).

The term fish is used in a wider and a narrower sense. In the first it includes any aquatic vertebrate swimming by means of fins and breathing by gills; in the more strict sense, as used here, it means aquatic branchiate forms with vertebral column, cranium, and well-developed visceral skeleton; with paired as well as unpaired fins, these supported by a cartilaginous or bony skeleton in addition to horny rays; with double nasal pits; with a skin and oral mucous membrane which can produce ossifications, the scales and teeth. The cyclostomes are thus excluded. The fishes are the best adapted of all vertebrates for an aquatic life, and their whole organization must therefore be considered from this standpoint.

The epidermis consists of numerous layers of protoplasmic cells with an extremely thin external cuticle. Cornifications of this epidermis are lacking under ordinary conditions, with the exception of a thin portion of the external subcuticular layer. At the time of sexual maturity cornifications increase greatly in most Cyprinoids and many Salmonids, producing hard bodies in the skin, the 'pearl organs.' Enormous numbers of large slime cells give the fishes their well-known slippery skins. Since the epidermis contributes nothing to the firmness of the body walls, all protective structures arise from the derma, which is composed of many layers of dense connective tissue and furnishes the characteristic dermal skeleton, the scales. These lie at the boundary of epidermis and derma, commonly imbedded in pockets of the latter, and are, on account of their different structure, of systematic value, although the classification based entirely upon them is no longer retained.

The placoid scales (fig. 554, 587, *4*) have already been mentioned, because they form the starting point for dermal ossifications and teeth (p. 515). They are rhombic bony plates, usually close together like a mosaic, but not overlapping. In the centre of each is a spine, directed backwards, in which is a pulp cavity, while the tip of the spine is covered with a cap of hard substance, variously called enamel or vitrodentine.

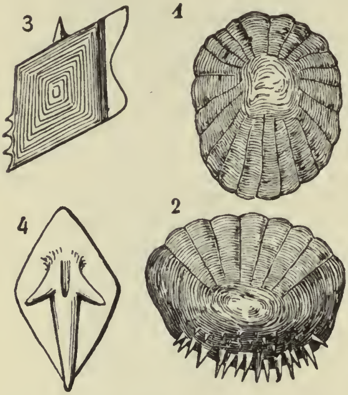


Fig. 587.—Scales of fishes. *1*, cycloid; *2*, ctenoid; *3*, ganoid; *4*, placoid.

The ganoid scales (fig. 587, *3*) are usually rhomboid and arranged like parquetry. In the early stages they may bear teeth, but these are lost in the adult. The outer surface is always covered with a thick layer of 'ganoin,' which gives, even in fossils, an iridescent effect, a most characteristic feature. The ganoin is no longer regarded as enamel, but the most superficial layer of dentine (vitrodentine).

Cycloid and ctenoid scales are closely related. They are always more loosely placed in the pockets, from which they are easily withdrawn as in 'scaling' a fish. They are arranged in oblique, transverse, and longitudinal rows, and overlap like shingles, one scale covering the parts of two scales behind. The cycloid scales (fig. 587, *1*) are approximately circular with a middle point, surrounded by concentric lines, from which go radiating lines. The ctenoid scale (*2*) has the radial and concentric lines of the cycloid, but has the hinder edge truncate and the free portion bearing small spines or teeth, processes of the concentric ridges.

Besides these types of scales many fishes bear considerable spines (strongly developed single scales) and larger bony plates, these last usually resulting from the fusion of numerous scales.

The coloration of fishes is threefold in origin. The silvery lustre is due to crystals of guanin which occur not only in the skin but in the peritoneum and pericardial walls. In some fishes from their iridescence (*Alburnus lucidus*) these crystals become of commercial value. They are freed from the skin by boiling with ammonia and, suspended in the fluid, form the important part of essence of pearl (essence d'orient) which is used in making artificial pearls, being either applied to the outside of alabaster balls (Roman pearls) or as a coating to the inside of glass beads (Paris pearls). The other colors of fishes are due in part to the numerous strongly pigmented fat cells, in part to 'chromatophores' in the derma, which, under control of the nervous system, can alter their form and extent and thus produce color changes in the fish. It is by means of these chromatophores that fishes adapt themselves to their surroundings. It is of interest to note that destruction of the eyes results in loss of power to change color.

The axial skeleton shows many conditions which are unknown outside the class, and varies in character from group to group, the most important differences consisting in its cartilaginous or bony character. The vertebræ are nearly always amphicœlous, the notochord persisting in the cavities between the successive centra (fig. 557). Neural and hæmal arches occur, these having as keystones the unpaired spinous processes. The neural arches extend throughout the columns; the hæmal are complete only in the tail; in the trunk the hæmal spines are absent and the hæmal processes, divided into basal processes and ribs, surround the viscera. A sternum is everywhere lacking. When ossification is lacking or is incomplete, two pairs of arches may occur in each segment, the anterior being the stronger and alone persisting in fishes with ossified vertebræ; the second is much smaller, so that its elements are not called arches, but intercalaria (figs. 556, 588).

The great number of visceral arches, and their independence from the cranium, are characteristic of fishes. After removal of these the cranium in all cartilaginous fishes is very simple (fig. 588), but in the teleosts, with the appearance of ossification, becomes very complicated, since the bones are very numerous and are not, as in mammals, in part fused to larger bones. There are also great differences between the different families of fishes, some having bones which are lacking in others (figs. 560, 589). The large membrane bones of the cranial roof (parietals, *p*, frontals, *f*, and nasals, *na*) and the large ventral parasphenoid (*ps*) are especially constant. The vomer in front of the parasphenoid is unpaired, while in all other vertebrates it is paired. Most constant of the cartilage bones are the ethmoids (the paired ectethmoids, *ee*, and the sometimes paired mesethmoid), and the four occipitals. On the other hand the otic and optic regions vary considerably; the otic region, from its great size, has several bones, usually (fig. 589) five in number: pterotic, *pto*, often called squamosal; sphenotic, *spho*, frequently called postfrontal; epiotic, *epo;* prootic, *pro;* and opisthotic, *oo*, the last sometimes lacking. In the region of the eye the cartilaginous sphenoids are rarely well developed, the large parasphenoid taking their place. The same is true of the ali- and orbitosphenoids, these sometimes forming an interorbital septum (fig. 560) or a more or less wide interorbital fenestra (fig. 589).

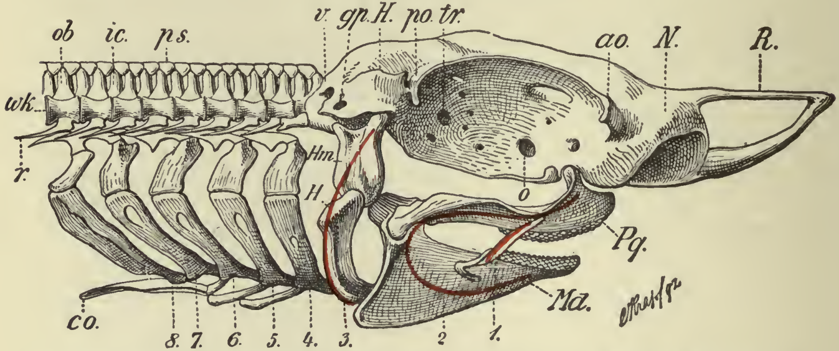


Fig. 588.—Cranium, visceral arches, and part of vertebral column of *Mustelus vulgaris*. *ao*, antorbital process; *co*, copula; *gp*, foramen for glossopharyngeal; *H*, otic capsule and hyoid; *Hm*, hyomandibular; *ic*, intercalare; *Md*, mandible (Meckel's cartilage); *N*, nasal capsule; *o*, optic foramen; *ob*, neural arch; *po*, postorbital process; *Pq*, pterygoquadrate; *ps*, spinous process; *R*, rostrum; *r*, ribs; *tr*, trigeminus foramen; *v*, vagus foramen; *1–8*, visceral arches: *1*, labial; *2*, mandibular; *3*, hyoid; *4–8*, gill arches.

The character of the visceral skeleton is related to the aquatic life. All fishes have numerous gill arches (five to seven, mostly five), which, since their function—gill supporting—is similar, are similar in structure. So far as they are not degenerate they consist each of four parts and are connected by unpaired copulæ, these often being fused. The upper ends are frequently toothed and, in chewing, are opposed by the rudimentary last arch, on which account these are spoken of as the superior and inferior pharyngeal bones. The anterior visceral arches are greatly different in cartilaginous and bony fishes. In the former (fig. 588) the pterygoquadrate (*pq*) and the Meckelian cartilage bear teeth and oppose each other in biting. In the bony fishes (fig. 589) the teeth of the lower jaw oppose the tooth-bearing elements, premaxillary and maxillary, of the maxillary series, while the pterygoquadrate elements—the palatine and the series of pterygoids—are the antagonists of the hyoid.

A second characteristic of the bony fishes is already outlined in the cartilaginous fishes: the modification of the hyomandibular to a suspensor of the jaws. In the elasmobranchs (especially the skates) the parallelism of hyoid and mandibular arches is lost, the hyomandibular separating from the hyoid and attaching itself to the hinge of the jaws. In the teleosts the hyomandibular is thus brought in connexion with the quadrate, and lies between it and the cranium, the joint being thus indirectly supported from the cranium, a bone, the symplectic (known only in fishes) helping out the suspensor, while another bone, the interhyal, connects this with the hyoid, which itself divides into two, so that the hyoid arch, like a gill arch, consists of four elements.

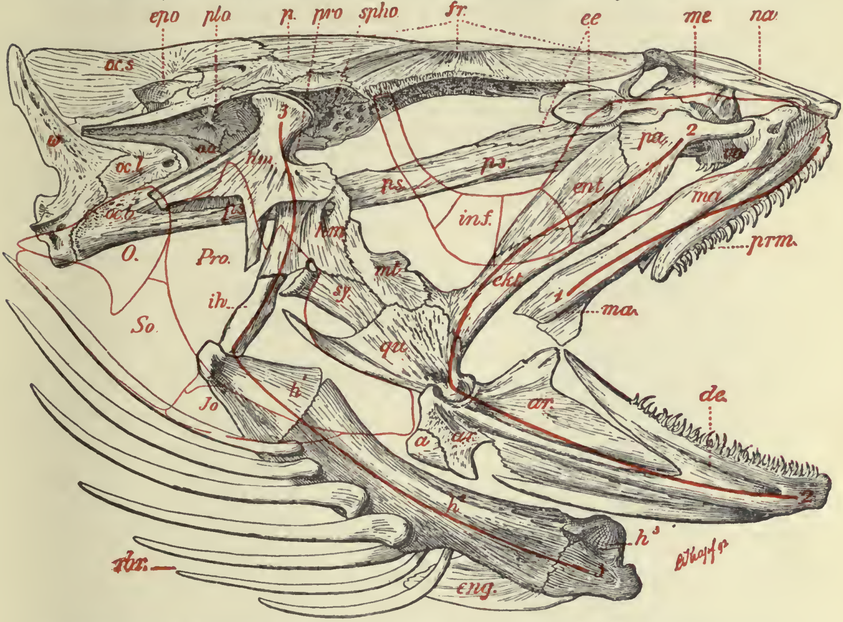


FIG. 589.—Skull of haddock. Infraorbital ring and operculum outlined in red. *a*, angulare; *ar*, articulare; *as*, alisphenoid; *de*, dentary; *ee*, ectethmoid; *ekt*, ectopterygoid; *eng*, os entoglossum; *ent*, entopterygoid; *epo*, epiotic; *fr*, frontal; h^1-h^3, hyoid elements; *hm*, hyomandibular; *ih*, interhyal; *ma*, maxilla; *me*, mesethmoid; *mt*, metapterygoid; *na*, nasal; *ocb*, *ocl*, *ocs*, basi-, ex-, and supra-occipital; *oo*, opisthotic; *p*, parietal; *pa*, palatine; *prm*, premaxillary; *pro*, prootic; *ps*, parasphenoid; *pto*, pterotic; *qu*, quadrate; *rbr*, branchiostegals; *spho*, sphenotic; *sy*, symplectic; *vo*, vomer; *w*, vertebra. Bones outlined in red: *inf*, infraorbital; *io*, interoperculum; *o*, operculum; *pro*, preoperculum; *so*, suboperculum; *1*, *2*, *3*, axes of labial, mandibular, and hyoid arches.

The opercular apparatus does not occur in all fishes. It is a number of bony plates and processes which arise from the hyoid arch and extend backwards over the gills, protecting them. It arises in part (opercular bones—*O*, *Pro*, *So*, *Io*, fig. 589) from the hyomandibular, in part (branchostegal rays) from the hyoid bone. The significance of this apparatus will be spoken of in connexion with the gills; it gives the fish head a definite character, but covers its structure, on which account it, like the infraorbital ring, is shown in red in the figure 589.

The appendages are also influenced by the aquatic life. In contrast to the cyclostomes, there are two pairs of paired fins, the thoracic or pectoral, and the pelvic, ventral, or abdominal fins; in contrast with Amphibia, reptiles, and mammals, which occasionally have fin-like structures, the fishes have three unpaired fins, dorsal, caudal, and anal fins. Only rarely, as in the eels, the ventral fins are lacking; more rarely (Muræenidæ) the pectorals are lost. The function of the fins in swimming and in balancing makes it necessary that they be broad and well-supported plates. Hence it is that numerous skeletal parts are present; besides those preformed in cartilage, numerous horny or bony rays; further, that all parts should be similar and closely, even if flexibly, bound to each other. Joints are unnecessary except at the base where the fins join the supports and move upon the body. The supports of the paired fins are the girdles, arched skeletal parts, which in the sharks are held only by muscles, a statement which is true for the pelvic girdle of all fishes. This is why the ventral fins so readily change their place. Their primitive position is at the hinder end of the body cavity (Pisces abdominales, figs. 598, 601). From this point they can move forward to beneath the pectorals (Pisces thoracici, fig. 602), or may even come to lie in front of them (Pisces jugulares) in the throat region (fig. 606). The pectoral arch is united to the vertebral column in the skates; to the skull by a series of bones in the teleosts.

The dorsal and anal fins are supported by elements preformed in cartilages which rest upon the neural or hæmal spines and in turn support the fin rays. In the caudal fin the rays rest directly upon the spinous processes. Three types of caudal fin are recognized—diphycercal, heterocercal, and homocercal (fig. 10), distinctions of great importance. The primitive type is the diphycercal, in which the vertebral column extends directly into the middle of the fin, dividing it into symmetrical halves. In the heterocercal type the vertebral axis binds slightly upwards at the base of the fin, so that the dorsal part is reduced, the ventral greatly enlarged, the result being extremely asymmetrical, as seen from the exterior. The homocercal fin is symmetrical externally, but in reality is extremely asymmetrical. The end of the vertebral column, the unossified notochord, is bent abruptly upwards, and hence the fin is almost entirely formed of the ventral portion, which is usually divided by a terminal notch into upper and lower halves. The homocercal fin begins with a diphycercal and passes through a heterocercal stage in development.

In correspondence with the simple motions the musculature is simple and consists largely of longitudinal muscles divided into myotomes, which are conical with the apex in front, and are so inserted in each other that a cross-section gives concentric circles. In a section there are at least two such systems, the muscles being divided by a lateral incision into dorsal and ventral halves. There are also smaller groups of muscles related to fins, gill arches, jaws, etc., but of much smaller size, derivatives from the larger mass. Electric and pseudelectric organs, which occur in different fishes, sometimes in the trunk, at others in the tail, are formed by the modification of muscles. Each organ consists of numerous closely packed vertical or horizontal columns, each column, like a Voltaic pile, consisting of layers of gelatinous plates (equivalents of muscle bundles) in which the nerves, with special end plates, terminate. The discharge is electronegative.

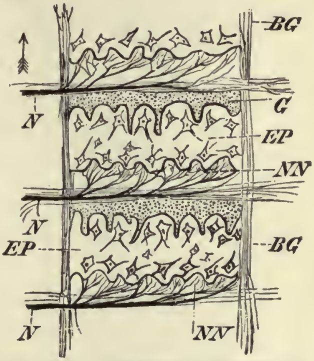


FIG. 590.—Driagrammatic section of electrical apparatus. (From Wiedersheim.) The arrow points dorsally or anteriorly. *BG*, connective-tissue framework; *EP*, electrical plates; *G*, gelatinous tissue; *N*, nerves entering through the septa; *NN*, nerve terminations.

The brain shows the low position of the class in the slight development of the cerebrum (fig. 591). This is especially true of the teleosts, in which, in place of a cortex, there is only a thin epithelial layer (*Pall*), what was formerly called cerebrum being only the corpora striata. The independent olfactory lobes lie either close to the cerebrum (most teleosts, *Lol*) or are separated from it by an olfactory tract (fig. 592, *h*). The optic thalami are small (*d*), but below them are enlargements characteristic of fishes, the lobi inferiores, and between them the sacculus vasculosus. Both optic lobes and cerebellum are greatly developed.

The nose consists of two preoral pits, the opening being divided by a bridge of skin into anterior and posterior nostrils. In many selachians the nostrils are connected with the mouth by a groove covered by a fold of skin, and in the Dipnoi there is a choana. The eye has several peculiarities. The lens is very convex, almost conical, due to the slight refraction caused by the passage of light from the water into the cornea. Further, the eye is very short-sighted because light is so absorbed by water that objects forty feet away are invisible. With this is connected the campanula Halleri. The processus falciformis, a sickle-shaped outgrowth of the choroid, extends from the entrance of the optic nerve into the vitreous body as far as the lens, swelling out into the campanula; this contains a muscle which draws back the lens and so is an apparatus of accommodation. Near the entrance of the optic nerve is a problematic organ, the choroid gland, consisting largely of blood-vessels (rete mirabile). Chondrifications and ossifications of the sclera are common. Lids are weakly developed or absent, and only some elasmobranchs have a nictitating membrane.

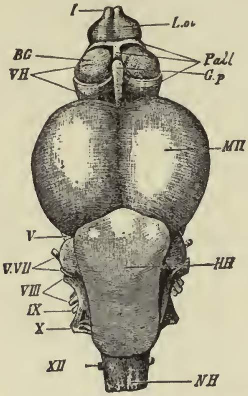


FIG. 591.

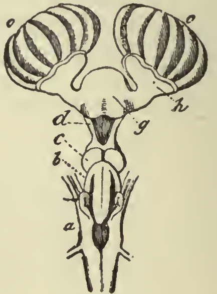


FIG. 592.

FIG. 591.—Brain of trout. (After Wiedersheim.) *BG*, corpus striatum; *GP*, pinealis; *HH*, cerebellum; *Lol*, olfactory lobes; *MH*, optic lobes; *NH*, Medulla oblongata; *Pall*, pallium, in part cut away; *VH*, cerebrum; *I–XII*, nerves. (See p. 536.)

FIG. 592.—Brain and nasal capsules of *Scyllium catulus*. (From Gegenbaur.) *a*, medulla; *b*, cerebellum; *c*, optic lobes; *d*, 'twixt brain; *g*, cerebrum; *h*, bulbus and tractus olfactorius; *o*, nasal capsules.

The ear has a relative size found in no other vertebrates, the labyrinth corresponding well with fig. 575. The labyrinth contains in many teleosts two otoliths, the asteriscus and sagitta, the first being especially large. Experiments show that the ears are primarily for balance, and hearing is doubtful. Strychninized fish do not respond to sound, if in its production mechanical vibrations are avoided.

Of all sense organs the most noticeable are those of the skin, especially those of the lateral line, which are nowhere else so well developed and which occur elsewhere only in cyclostomes and aquatic amphibia. In fishes a line on either side usually begins at the tail and extends to the head, where it divides into several curved lines (fig. 602, *Sl*). Its position is marked by a groove or a canal in the scales which opens to the exterior by numerous canals through the scales. Branches of trigeminus, facialis, glossopharyngeus, and especially the lateral branch of the vagus (fig. 570) go to these organs, the latter extending back to the tail. These supply special sense organs, which may be grouped in several lines or occur in pits (ampullæ) in the skin in other places. Their function is obscure, since nothing of the sort occurs in man or mammals. They are specific organs of aquatic vertebrates and possibly have to do with the perception of water pressure.

The alimentary tract is spacious only in the oropharyngeal region. Then it narrows to a tube in which the various regions are not sharply marked off from each other. Mouth and pharynx frequently bear teeth. In the teleosts the bones of the floor of the cranium and those of the visceral arches may be covered with coalesced heckel-like teeth. In the elasmobranchs the teeth are mostly confined to the lower jaw and the pterygoquadrate, but are in rows, the anterior row alone being functional; but as these are loosely held they are easily torn out, when they are replaced by the row behind. Liver and spleen are always present; pancreas and gall bladder usually occur. In many fishes blind sacs, the pyloric cæca, occur at the junction of stomach and intestine (fig. 593, *B*); others have a spiral valve (*A*), a fold of mucous membrane, which extends like a spiral stairway into the lumen of the intestine, increasing the digestive surface. Cæca and spiral valve rarely occur in the same fish.

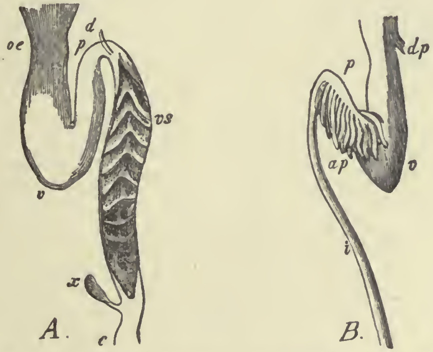


FIG. 593.—Digestive tracts of (*A*) *Squatina vulgaris* (partly opened) and (*B*) *Trachinus radiatus*. (From Gegenbaur.) *ap*, pyloric cæca; *c*, rectum; *d*, bile duct; *dp*, duct of air bladder; *i*, intestine; *oe*, œsophagus; *p*, pylorus; *v*, stomach; *vs*, spiral gland; *x*, rectal gland.

Gills of two types occur (fig. 594, *A* and *B*). In both the gill clefts, which lie between successive branchial arches, begin by openings in the pharynx, but differ in their external openings. In the elasmobranch type (*A*) the external openings are a series of slits separated by broad dermal bridges which cover the gills and gill clefts (fig. 598). The gills are vascular folds of mucous membrane with secondary folds which extend on anterior and posterior sides of the cleft. Each arch except the last, as the sections (fig. 594, *A*, and 595) show, bears two rows of gill folds (demibranchs) which belong to different clefts and are separated from each other by tissue containing the cartilaginous gill rays.

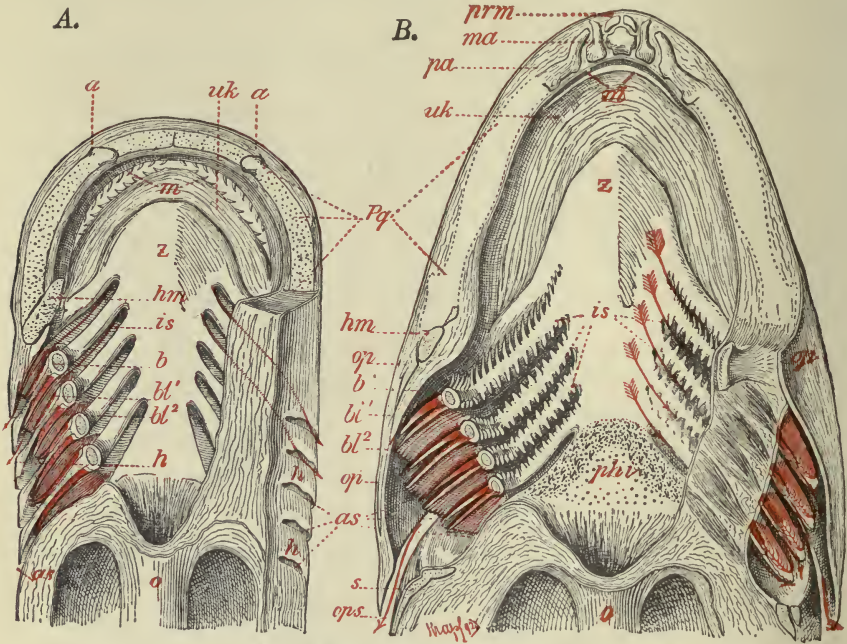


FIG. 594.—Pharynges of (*A*) Elasmobranch (*Zygæna*) and (*B*) Teleost (*Gadus*), the skull removed and on the left the gill slits cut across. *a*, attachment of upper jaw to cranium; *as*, outer gill slit; *b*, gill arch; bl^1, bl^2, anterior and posterior gills (demibranchs); *h*, dermal projection; *hm*, hyomandibular; *is*, inner gill cleft; *m*, mouth; *ma*, maxillare; *o*, œsophagus; *op*, operculum; *ops*, opercular opening; *pa*, palatine; *phi*, inferior pharyngeal bones; *pq*, pterygoquadrate; *prm*, premaxilla; *s*, shoulder girdle; *uk*, lower jaw; *z*, tongue.

In the second type (*B*), which occurs in all other fishes, the dermal bridges are lacking, and the tissue between the demibranchs has more or less completely disappeared, so that the demibranchs of one arch become connected, their free ends projecting into the water like the teeth of a double comb. Here, on account of their very delicate structure, they would be exposed to serious injury were they not protected by the operculum or gill cover. This is a fold of skin arising from the hyoid arch and extending back over the gill region. It is supported by two groups of bones, the opercular bones proper (fig. 589, *O*, *So*, *Io*, *Pro*), attached to the hyomandibular, and the branchiostegals (*rbr*) from the hyoid, these latter supporting the branchiostegal membrane. Between the free edge of the operculum and the branchiostegal membrane and the skin of the body behind is the opercular cleft (fig. 594, *ops*), which is obviously not identical with a gill cleft, but leads into an atrium into which the gill clefts empty. In many elasmobranchs and ganoids there is a rudimentary cleft, the spiracle, between the pterygoquadrate and hyomandibular, in which a rudimentary gill, or pseudobranch, may occur, this often persisting when the spiracle is closed.

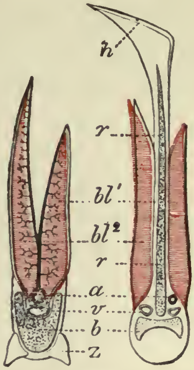


Fig. 595.—Sections of gill arches of *Gadus* (left) and *Zygæna* (right), slightly enlarged. *a*, artery; *b*, gill arch; bl^1, bl^2, demibranchs; *h*, dermal projection; *r*, cartilage ray; *v*, vein; *z*, tooth.

Besides gills, fishes, with the exception of elasmobranchs and some teleosts, have a swim bladder which is usually regarded as the homologue of the lungs. It is often shaped like an hour glass, filled with air, and may open into the œsophagus by a pneumatic duct (Physostomi), or this, appearing in development, may be lost in the adult (Physoclisti). The air bladder serves for respiration in the Dipnoi and possibly in some ganoids (*Lepidosteus* and *Amia*), but is usually a hydrostatic apparatus, its enlargement or compression altering the specific gravity of the fish. In fishes brought up from great depths the expansion of air in the swim bladder frequently forces the viscera out through the mouth.

The heart, enclosed in the pericardium, lies immediately behind the gill region, and is protected by the shoulder girdle. It always consists of auricle and ventricle (fig. 596), separated by a pair of valves to prevent back-flow of the blood; it sends the blood to the gills by the arterial trunk (ventral aorta), and receives it from the body through a thin-walled sac, the venous sinus, in which the hepatic veins and the Cuvierian ducts (formed by union of jugular and cardinal veins) empty (figs. 65, 597).

The most important differences lie in the development of conus and bulbus arteriosus. These are muscular accessory organs, the first arising from the heart, the other from the arterial trunk; and correspondingly the conus has striped, the bulbus smooth muscle fibres. The anterior end of the heart contains 'semilunar' valves, which, like the auriculo-ventricular valves, prevent the back-flow of the blood. When, by increase in the number of valves, this part becomes elongate, a conus arteriosus (fig. 596, *A*) is formed. The bulbus (C) is a muscular swelling in front of the conus, in the arterial trunk.

The connexion of ventral and dorsal aortæ is effected in young fishes (fig. 597) by the gill arteries directly; later by means of the complicated loops of the gill circulation. When these are developed, afferent branchial arteries, gill capillaries, and efferent arteries can be recognized, the latter uniting to form the dorsal aorta and also giving off the arteries (carotids), which go to the head.

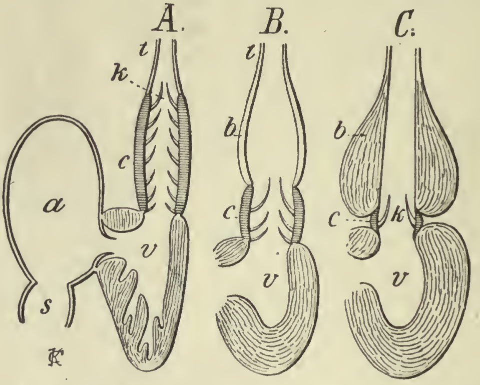


Fig. 596.—Forms of hearts of fishes in schematic long section. (After Boas.) A, selachian and most ganoids; B, *Amia;* C, Teleost. a, auricle; b, bulbus arteriosus; c, conus arteriosus; k, valves; s, sinus venosus; t, truncus aortæ; v, ventricle.

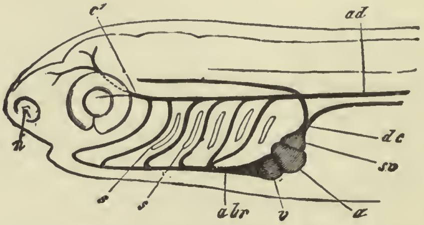


Fig. 597.—Head of embryo teleost. (Diagram from Gegenbaur.) a, auricle; abr, ventral aorta with arterial arches; ad, dorsal aorta; c, carotid; dc, Cuvierian duct, formed by union of jugular and posterior cardinal veins; n, nostril; s, gill clefts; sv, sinus venosus; v, ventricle.

The nephridia are a pair of large reddish-brown organs lying outside the body cavity to the right and left of the vertebral column, usually extending from heart to anus. Their ducts empty behind the anus or in the dorsal wall of the intestine and are often provided with enlargements called, from their functions, urinary bladders, although totally different morphologically from the urinary bladder of the higher vertebrates. The gonads, suspended by mesorchia or mesovaria, are large and project into the body cavity. They are rarely unpaired. In the elasmobranchs and most ganoids their products pass out by the urogenital system (p. 552), in other forms by the pori abdominales or by special ducts.

Cuvier divided the fishes into cartilaginous and bony groups, an important step so far as the extremes (elasmobranchs and teleosts) were concerned. Agassiz recognized a middle group which he named Ganoidei, from the character of the scales, but his account was modified and made more accurate by Johannes Müller, who also included the Dipnoi among the fishes. At present the group of ganoids is retained largely as a matter of convenience. Its members are more closely related with the teleosts than with the elasmobranchs, and in America Ganoids and Teleosts are united under the head Teleostomi, the name alluding to the presence of a true upper jaw comparable to that found in higher vertebrates.

Sub Class I. Elasmobranchii (*Plagiostomi, Chondropterygii*).

The elasmobranchs, the shark-like fishes, are almost exclusively marine, varying in length from a foot and a half to sixty feet, living almost exclusively on other vertebrates, and noted for their voracity. Sometimes slender and cylindrical, as in the sharks (fig. 598), sometimes flattened dorsoventrally, as in the skates (fig. 599), they agree in form in that the head is prolonged into a snout, which is usually supported by a cartilaginous prolongation of the cranium, the rostrum (fig. 588, *R*). The mouth lies ventrally, at more or less distance from the anterior end, and is transverse, whence the name Plagiostomi—transverse mouth. This position makes it necessary that a shark approaching its prey from below must turn on its back before biting. The tail is heterocercal or is drawn out in a long filament. The skin is covered with placoid scales, usually close together, these being so small in some cases that the skin—shagreen—is used instead of sandpaper for polishing. More rarely the scales are larger, and the spines, which project from the skin, justify in size and form the term dermal teeth. Such strong spines occur especially at the front of the

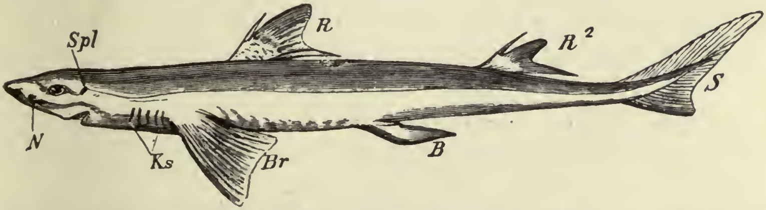


FIG. 598.—*Acanthias vulgaris*,* dogfish. (From Claus.) *B*, ventral fin; *Br*, pectoral fin; *Ks*, gill clefts; *n*, nostril; R', R^2, dorsal fins; *S*, heterocercal caudal fin; *Spl*, spiracle.

dorsal fins (ichthyodolurites of paleontologists). The skeleton is cartilaginous, frequently calcified on the outside. The calcification can also extend into the vertebræ, producing star-like figures. Since bone is lacking, the sharks have no upper jaws, but bite with the pterygoquadrate. The amphicœlous vertebræ (lacking in the Holocephali and the extinct Cladoselachii, Ichthyotomi, and Acanthodidæ), have neural arches, small ribs, and intercalaria. The number of gill arches and clefts varies between five and seven, the first cleft lying between the hyoid and the first branchial arch. Besides, most elasmobranchs have a spiracle and pseudobranch (fig. 598, *Spl*). Except in the Holocephali the gill clefts open separately, the hyoid arch being without an operculum.

In the visceral anatomy these points are of importance as distinguishing elasmobranchs from Teleostomes. (1) The heart has a large conus, with several rows of valves (fig. 596, *A*), but lacks a bulbus. (2) The alimentary tract (fig. 593, *A*) has a spiral valve, but lacks swim bladder and pyloric cæca. (3) The sexual products are carried to the exterior by the urogenital ducts. The eggs escape from the follicles of the ovary (occasionally unpaired) by dehiscence into the body cavity, and from thence by the unpaired ostium tubæ and the paired Müllerian ducts to the exterior. The spermatozoa traverse the anterior part of the Wolffian body ('kidney'). Sexual and reproductive ducts open dorsally into the cloaca.

Male elasmobranchs are distinguished by the presence of a copulatory structure (mixipterygium) developed by enlargement of some radii of the ventral fin (fig. 599, *c*). The large eggs, rich in yolk, are fertilized in the oviducts and usually develop in uterine enlargements of the ducts. The embryos (fig. 582), with long gill filaments protruding from the gill slits, are nourished by the yolk in the yolk sac. In *Mustelus* and *Carcharias*, as Aristotle knew, there is the formation of a placenta, which differs from that of the mammals in that the embryonic blood supply arises from the blood-vessels of the yolk sac and are not allantoic. There are oviparous elasmobranchs, and in these the egg is surrounded by albumen and a shell, but these eggs differ from those of birds in that the skull is horny and is usually drawn out at the four corners, sometimes with threads for attaching the egg to plants, etc.

Order I. Selachii.

With the notochord more or less completely replaced by vertebral centra; no dermal bones.

Sub Order I. DIPLOSPONDYLI. Gill slits lateral, six or seven in number, a single dorsal fin. *Chlamydoselachus* with terminal mouth. *Hexanchus*,* mouth normal, six gill slits; *Heptanchus*, seven gill slits.

Sub Order II. SQUALI (Euselachii). Normal sharks, with cylindrical bodies, free thoracic fins, heterocercal tail, lateral gill slits. Most of them are fast swimmers and are rapacious, the teeth being usually pointed, with sharp or toothed edges, but in some the teeth are pavement-like and are used for crushing shell fish. The numerous families are distinguished by vertebral characters, number of dorsal fins, presence of nictitating membrane, etc. In the GALEIDÆ, in which the nictitating membrane is present, belong, besides the dog-sharks (*Mustelus* * and *Galeus* *), the largest of all sharks, *Carcharinus*,* some of which have man-eating reputations. The hammer heads (*Zygœna* *) are closely allied. The mackerel sharks *Lamna* *) and the great white 'man-eater,' *Carcharodon*,* lack nictitating membranes. All of the foregoing have star-shaped figures in the vertebræ (p. 570). In the dog-fishes, represented by *Acanthias vulgaris* * (or *Squalus acanthias*, fig. 598), there is a spine in front of each dorsal fin.

Sub Order III. RAIÆ. In the skates the body is flattened horizontally fig. 599), and the pectoral fins, also flattened, are united to the sides of the body, the union usually extending clear to the tip of the snout, and frequently back to the pelvis, giving the body a rhombic appearance from above. The animals swim by undulating motions of these fins. They mostly lie quiet on the bottom, and hence the lower surface is white, the upper colored. The union of the fins to the side has resulted in trans-

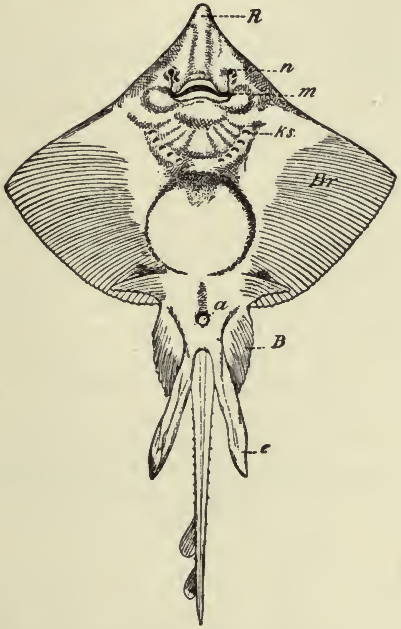


FIG. 599.—*Raia batis*, male, ventral view. (After Möbius and Heincke.) *B*, ventral, *Br*, pectoral fin; *R*, rostrum; *a*, anus; *c* copulatory part of ventral; *ks*, gill clefts; *m*, mouth; *n*, nostril; between them the oronasal groove.

fer of the gill slits to the lower surface, the spiracles to the upper. The teeth are usually pavement-like. The PRISTIDÆ, or sawfishes, are the most shark-like, but are readily recognized as belonging here by the position of the gill slits. The common name is due to the fact that the snout is prolonged into a paddle-shaped blade, the edges armed with teeth. *Pristis.** RAIIDÆ; the typical members of the group; *Raia.** Closely allied are the TRYGONIDÆ, or sting rays, with whip-like tail with one or two spines, the 'stings,' at the base; *Dasyatis.** The torpedos (TORPEDINIDÆ) have smooth skins, and have electrical organs, kidney-shaped bodies, on either side between gill arches and pectoral skeleton. *Torpedo.**

Order II. Holocephali.

These forms, which have no common English names, differ from the selachii in having the pterygoquadrate arch, which bears a few large chisel teeth, fused with the cranium without a suspensor; in having a dermal fold constituting an operculum, which covers the gill slits; and corresponding with this, the gills more on the teleost type (p. 566). Lastly, the vertebral centra are not developed. *Chimæra.** Fossils appear in the Devonian.

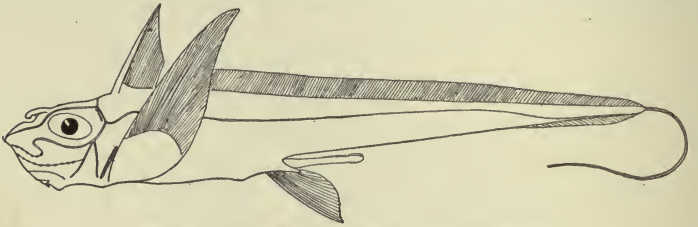


FIG. 600.—*Chimæra monstrosa.* (From Kingsley.)

The CLADOSELACHII (*Cladoselache*), ICHTHYOTOMI (*Pleuracanthus*), and ACANTHODIDÆ are paleozoic forms in which vertebral centra were lacking. In *Cladoselache* the skeleton of the paired fin consisted of numerous similar radii and was more primitive than the archipterygium; *Pleuracanthus* was diphycercal, and the head, as in *Acanthodes*, bore dermal bones.

Sub Class II. Ganoidei.

The ganoids form a transition group in which elasmobranch and teleost characters are mingled in a notable manner. They have the spiral valve of the sharks, the swim bladder of the telosts; the heart with the conus is selachian, the respiratory structures—the comb-like gills and the operculum—are as distinctly teleostean. The hyoid arch, with the development of the operculum, has not entirely lost its respiratory function, since in garpike and sturgeon it bears an opercular gill, and often there is a pseudobranch in the spiracle. The skeleton is always ossified in certain parts; large membrane bones lie on the shoulder girdle, on the roof and floor of the skull (parasphenoid); the horny threads of the fins are bony rays. In general the skeleton ranges between two extremes—an extremely primitive cartilaginous condition with persistent notochord, and one with a more than ordinary degree of ossification. It is important for the systematist to find characters in all ganoids which occur only in the group. The ganoid scales, used by Agassiz, are not sufficient, since the sturgeon has bony plates free from ganoin, while the paddle bill (*Polyodon**) has almost no dermal skeleton, and *Amia* has cycloid scales. Most recent and fossil forms possess fulcra, bony plates with forked ends lying shingle-like in front of the fins (fig. 10, *B*), but these are not universal, and are absent, *e.g.*, in *Amia* and *Polypterus* (fig. 10, *A* and *C*). The group is largely American. The few recent ganoids fall into three distinct groups.

Order I. Crossopterygii.

These are largely extinct, but two genera persisting to-day. The tails are diphycercal or heterocercal; the pectoral fins have the basal portion scaled; broad gular plates beneath the jaws in place of branchiostegals; the skeleton well ossified. *Polypterus* and *Calamoichthys* from Africa. The order was probably ancestral to the Amphibia.

Order II. Chondrostei.

These forms resemble the sharks externally in the heterocercal tail, spiracle, ventral position of the mouth; internally in the cartilaginous skull and (except *Polyodon*) in the pterygoquadrate serving as upper jaw. In the vertebral column they are more primitive than most selachians, since centra are lacking, the neural and hæmal arches and the intercalaria resting direct on the notochordal sheath (fig. 556). ACIPENSERIDÆ, with large bony dermal plates. *Acipenser*,* sturgeon. The swim bladder furnishes isinglass, the ovaries make caviare. POLYODONTIDÆ, with naked skin and long paddle-like snout, toothed maxillaries present. *Polyodon*,* paddle fish.

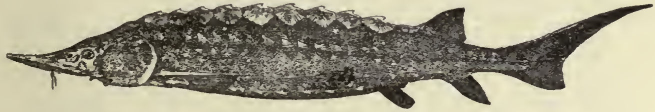


FIG. 601.—*Acipenser sturio*,* common sturgeon. (After Goode.)

Order III. Holostei.

In these the skull is ossified as in teleosts; maxillary and premaxillary bones are present, the pterygoquadrates reduced and not meeting in front, and the mouth terminal. The body may be covered either with ganoid or cycloid scales. The living forms (the group appears in the trias) have ossified opisthocœlous vertebræ and diphy- or homocercal tails.

LEPIDOSTEIDÆ. Scales rhomboid, branchiostegal rays present, a pseudobranch, but no spiracle. *Lepidosteus*,* garpike. AMIIDÆ, distinctly teleostean in appearance with cycloid scales, amphicœlous vertebræ, and heart with reduced conus (fig. 596, *B*). *Amia*,* bow fin.

Sub Class III. Teleostei.

The teleosts owe their name to the extensive ossification of the skeleton, which consists, in the trunk, of amphicœlous vertebræ, and in front a skull with numerous primary and secondary bones, already enumerated (p. 560, fig. 589). Maxillaries and premaxillaries are present, but these are frequently without teeth, since other bones of the mouth (vomers, palatines, hyoid, gill arches, superior pharyngeals—the latter alone in Cyprinoids) may bear teeth. Frequently there are present small bones, usually forked, lying in the intermuscular septa above the ribs, which are not preformed in cartilage. These are the epipleurals, and are distinct from the ribs. In the fins both cartilage and dermal rays are ossified, the former remaining small, the rays forming most of the support. These rays may either be soft and flexible (Malacopteri) or hard and spine-like (Acanthopteri), a matter of classificatory value. In the first case they consist of numerous small threads (fig. 602, *Br*, *A*, *B*, R_2), in the other the parts of a ray are fused to a spine which, sometimes provided with poison glands (*Scorpæna*, *Amphacanthe*, etc.), become good defensive weapons. The tail is usually homocercal; the diphycercy of eels and other fishes is secondary. The dermal skeleton consists of ctenoid or cycloid scales, sometimes of spines or body plates. In rare instances the skin is naked.

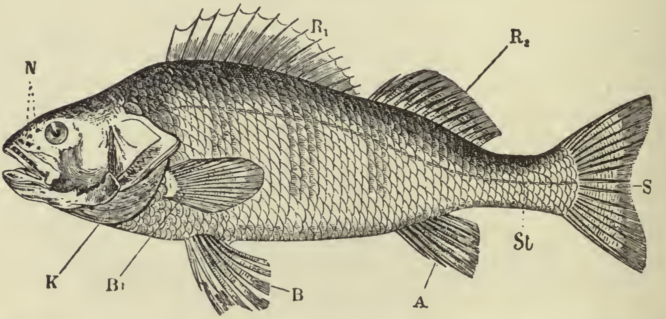


FIG. 602.—*Perca fluviatilis*. (From Ludwig-Leunis.) *A*, anal fin; *B*, ventral fin; *Br*, pectoral fin, *K*, operculum; *N*, nostrils; R_1, R_2, spinous and soft dorsal fins; *S*, caudal fin; *Sl*, lateral line.

The hyoid arch always bears an operculum and branchiostegal membrane, but there is no opercular gill. The gills of the comb-like type, are confined to the four anterior gill arches, but they may be reduced to even two and one-half pairs of demibranchs. Instead of a conus (present in *Butrinus*), the bulbus arteriosus is well developed; a spiral valve is lacking, but pyloric appendages are common. A swim bladder is usually present, but its duct is frequently closed.

The teleosts are distinguished from all vertebrates except the cyclostomes and perhaps some ganoids in that the nephridial system does not form part of the sexual ducts. The eggs and milt are deposited through the abdominal pores or by special canals developed from the body cavity. Copulation occurs in only a few viviparous forms (Embiotocidæ, *Gambusia*, etc.). The rule is that males and females deposit their reproductive products in the water at the same time, and this leads to the enormous schools of herring and other fishes which occur yearly at certain times. This also explains the ease with which artificial impregnation in fish culture is performed.

In rare instances the males care for the young, as in the case of the sticklebacks; more noticeable are the conditions in the lophobranchs (sea horses and pipe fish), where the males receive the eggs in a brood pouch on the ventral surface. A metamorphosis is known only in the eel-like fishes, the larvæ of which—originally described as distinct under the name *Leptocephalus*—are flat, transparent forms with colorless blood, enormous tails, and extremely small trunk. These larvæ normally occur in the sea at the depth of some hundred fathoms. The fresh-water eels go to the ocean for propagation. On the other hand many salt-water fish go to fresh water for reproduction.

The classification of the fishes is yet in an unsettled state, partly owing to the large number of forms, partly to the fact that the groups intergrade. Most European writers recognize six divisions, Physostomi, Anacanthini, Pharyngognathi, Acanthopteri, Chætognathi, and Lophobranchii. Our authorities separate the Ostariophysi from the Physostomi, the Pediculati and Hemibranchii from the Acanthopteri, and unite the Anacanthini and some of the Pharyngognathi with the Acanthopteri and make a distinct group, Synentognathi, of the others. The characters on which these divisions are based are less convenient for the tyro than those adopted here.

Order I. Physostomi.

The character to which this name refers is not readily seen without dissection, the persistence of the duct of the swim bladder. This is, however, correlated with the soft character of the fin rays (few exceptions) and the abdominal position of the ventral fins. The Ostariophysi are remarkable in having a chain of bones connecting the swim bladder with the ear. More than a third of the food fishes and nearly all of the fresh-water fishes belong here.

The Ostariophysial families are the SILURIDÆ (1000 species), or cat-fish, with barbles about the mouth, of which *Malapterurus*, the electric cat of Africa, is most noteworthy. The CYPRINIDÆ, or carp (1000 species), and the suckers, CATOSTOMIDÆ, have little food value. The electric eel of South America belongs to the GYMNONOTI. The other families are true Physostomes. The SALMONIDÆ are easily recognized by the 'adipose dorsal,' a fin formed of a fold of skin without fin rays. The trout and salmon (*Salmo* *) belong here and are among the most important food fishes. *Osmerus*,* smelt; *Coregonus*,* white fish; CLUPEIDÆ, herring, shad; ANGUILLIDÆ, eels, the breeding habits referred to above. ESOCIDÆ, pike and pickerel. AMBLYOPSIDÆ, blind fish of Mammoth Cave.

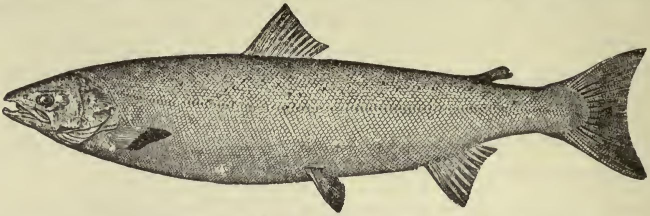


FIG. 603.—*Salmo salar*,* Atlantic salmon. (After Goode.)

Order II. Paryngognathi.

In many fishes the inferior pharyngeal bones (*i.e.*, the last rudimentary gill arch) fuse to form a single bone, and these forms are called Pharyngognathi. Some have spiny fins, among the LABRIDÆ, including *Ctenolabrus*,* the cunners, and *Tautoga*,* the tautog. These are placed among the Acanthopteri by American authors. Others have only soft fin rays. These are the Synentognathi and include the EXOCŒTIDÆ, or some of the flying fishes, in which the pectoral fins are very large, acting as parachutes when the fish leap from the water. *Exocœtus*.*

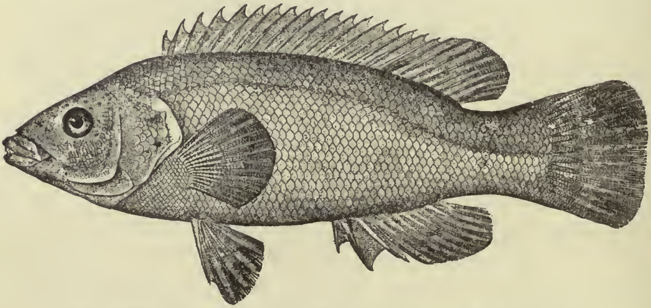


FIG. 604.—*Ctenolabrus cœruleus*,* cunner. (After Goode.)

Order III. Acanthopteri (Acanthopterygii).

This is the largest group of fishes, its members usually having the ventral fins thoracic in position and more than three rays spiny in dorsal, anal, and ventral fins. The sticklebacks (GASTEROSTEIDÆ) and some other forms have the pharyngeal bones reduced, the ventral fins farther back, and form the group Hemibranchii. *Gasterosteus.** The perch of fresh water (PERCIDÆ), *Perca** and *Micropterus** (black bass), and the marine SERRANIDÆ, some of which are hermaphroditic, have ctenoid scales. The SCOMBRIDÆ, with *Scomber*,* the mackerel, and *Thynnus*,* the horse mackerel, and the XIPHIIDÆ, or sword fishes, in which the snout is prolonged into a long sword, are the most important edible fishes of the group. The LORICATI, including the sculpins (*Cottus*,* *Hemitripterus*,*) frequently have the body armored with bony plates. The EMBIOTOCIDÆ, or surf perches of the Pacific, are viviparous. The suck fishes, *Remora*,* *Echeneis*,* have the first dorsal modified into a sucker on the top of the head.

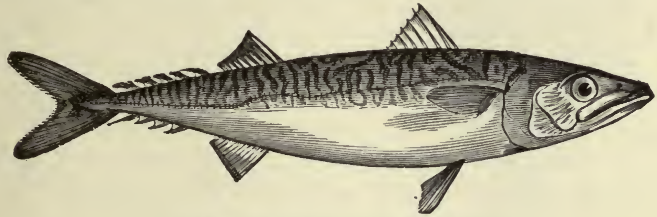


FIG. 605.—*Scomber scombrus*, mackerel.

Order IV. Anacanthini.

These are soft-finned fishes in which the ventral fins lie in front of the pectorals. Structure goes to show that these have descended from Acanthopteran forms. With few exceptions

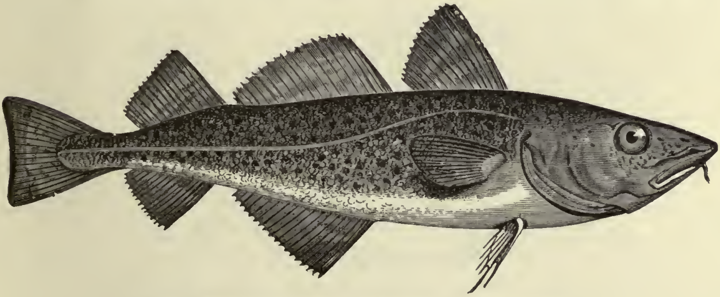


FIG. 606.—*Gadus morrhua*,* cod. (After Storer.)

(*Lota,** burbot), all are marine. The Gadidæ, with *Gadus,** including the cod and haddock, and the Pleuronectidæ, with *Hippoglossus,** the halibut and other genera, the flounders, turbot, and sole, make this the most important group of marine fishes. The Pleuronectidæ, from their asymmetry, need a word. The young are perfectly symmetrical, but the animals turn on one side, the lower becoming white. The eye of this side gradually works over to the upper side, twisting the bones of the skull in its progress.

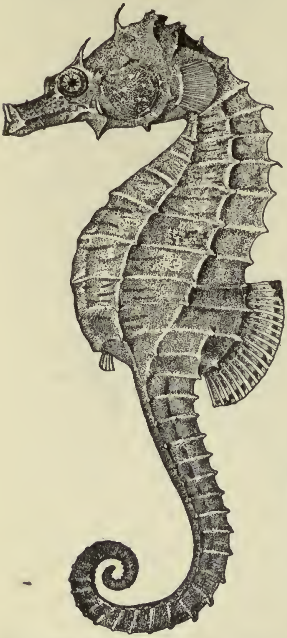


Fig. 607.—*Hippocampus heptagonus,** sea horse. (After Goode.)

Order V. Lophobranchii.

A small group of marine species, having in common gills composed of small rounded tufts, the body covered with a segmented armor of bony plates and peculiar breeding habits, the male carrying the eggs and young in a brood pouch. The sea horses, *Hippocampus,** with their horse-like heads, and the slender pipe fishes, *Syngnathus,** belong here.

Order VI. Plectognathi.

A small group of peculiar compact fishes, in which the bones in each jaw are coossified, the ventral fins reduced or absent. In the trunk fishes, Ostracodermi, the body is enclosed in a firm angular box of bony plates. The Gymnodonta, or swell fishes (fig. 608), have the power of inflating the body to spherical sacs. The flesh is poisonous.

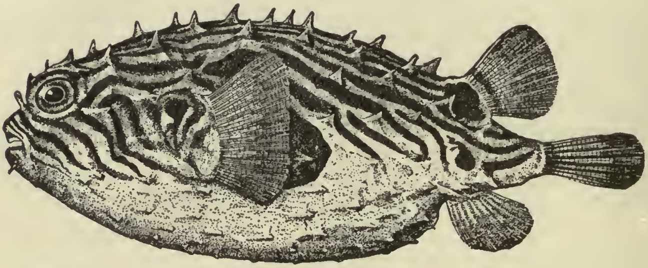


Fig. 608.—*Chilomycterus geometricus,** swell fish. (After Goode.)

Sub Class IV. Dipnoi (Dipneusti).

The lung fishes have the form of true fishes, with scales and paired fins, supported by a single or a doubly pinnate archipterygium. The median fin is not separated into dorsals, caudal and ventral, and the caudal part is diphycercal. The skeleton is very primitive, consisting largely of cartilage, the notochord being retained to a great extent. The animals live in fresh water and, under ordinary conditions, breathe by gills which are covered by an operculum. In the gills there are some peculiarities recalling amphibian structures, *Protopterus*, and the young of *Lepidosiren* having external as well as internal gills. The resemblances are strengthened by the periodic appearance of pulmonary respiration. The lung fishes live in the tropics in pools and swamps which, during the hot season, may be more or less completely dried up. When the water becomes too foul for branchial respiration, the swim bladder is used. This is a paired or unpaired sac with a duct leading to the œsophagus, and the interior has its respiratory surface increased by the development of air cells. *Protopterus* indeed can live out of water; it burrows in the mud at the dry season, and builds a cocoon lined with mucus in which it remains quiescent until the wet season. The nose is respiratory, with a choana opening into the mouth cavity. The last gill vessels give off pulmonary arteries, and there are veins carrying the blood back to the heart. The heart itself shows the beginning of division into arterial and venous halves, especially in the regions of the conus and auricle.

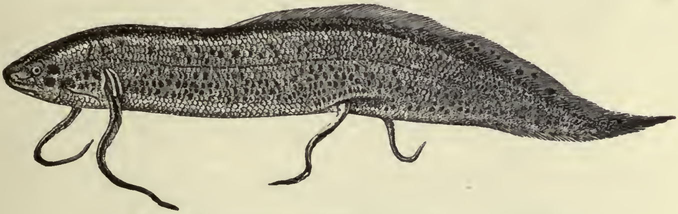


FIG. [illegible].—*Protopterus annectens*, lung fish. (From Boas.)

The few species now living have a wide and discontinuous distribution, and are the remnants of a much richer group which appeared in the paleozoic. MONOPNEUMONIA, with one swim bladder: *Ceratodus* of Australia. DIPNEUMONIA, with two bladders: *Protopterus*, Africa; *Lepidosiren*, South America. Possibly the paleozoic ARTHRODIRA, some of gigantic size (*Dinichthys*), belong here.

Class III. Amphibia.

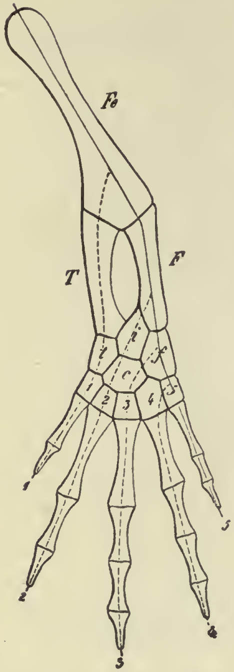


FIG. 610.—Skeleton of hind leg of *Salamandra maculosa*, larva. (From Gegenbaur.) *c*, centrale; *F*, fibula; *f*, fibulare; *Fe*, femur; *i*, intermedium; *T*, tibia; *t*, tibiale; *1-5*, carpalia and corresponding metacarpals and digits.

There are two views as to the origin of the Amphibia. According to the one they have descended from Crossopterygian ganoids (and this seems the better supported); the other is that they have come from the Dipnoi. The group is distinguished at once from the fishes by the absence of fins. There is, it is true, a median fin in larval life, and this may persist (Perennibranchs, *Triton*), but it is never divided into dorsal, caudal, and anal, and it lacks any skeletal support (figs. 4, 5). The paired fins are replaced by pentadactyle feet (p. 529). These are often webbed and are used for swimming; they are also used for creeping and leaping, and are consequently jointed between the separate skeletal elements (fig. 610). Besides the shoulder and hip joints, which alone occur in fishes, there occur also elbow (knee), wrist (ankle), and finger joints. The number of digits is not always five, for a reduction to four, three, or even two occurs.

The connexion of the girdles with parts of the axial skeleton (lacking in most fishes) is of importance. The pelvic girdle is connected with the vertebral column by means of the ilium, which articulates either directly or by a sacral rib with the single sacral vertebra. Ventrally the two halves of the girdle fuse, and usually the limits of ischium and pubis cannot be traced.

The attachment of the pectoral girdle is less firm (fig. 564, *A*). The dorsal portion, the scapula, ends free in the muscles; the ventral, differentiated into coracoid and clavicle, is often connected with the sternum, but this is not connected with the vertebral column, since the ribs are too short to reach it. The sternum is frequently connected with an episternum.

The vertebral column often (Perennibranchs, Derotremes, Cæcilians, and many Stegocephali) resembles that of fishes in amphicœlous centra and persistence of notochord. The notochord may disappear, there then occurring opisthocœlous (Salamandrina) or procœlous centra (most Anura). There is also an articulation of skull with vertebral column, rare in fishes but characteristic of land animals, by which the first vertebra (atlas) becomes distinct from the rest.

The skull is remarkable for the extent to which the chondrocranium is retained and the consequent small number of primary bones (figs. 611, 612). The bones of the orbital region are represented by a pair each of ali- and orbitosphenoids in the urodeles, by a ring of bone, the sphenethmoid (os en ceinture), in the anura. The auditory region usually contains only prootics, the occipital only exoccipitals. The absence of other occipitals is often of value in distinguishing between amphibian and reptilian skulls, since in the former the articulation with the atlas is consequently by double occipital condyles. Of secondary cranial bones are to be mentioned the nasals, frontals (in many prefrontals also), and parietals, the latter two fused in anura to frontoparietals; ventrally the large parasphenoids.

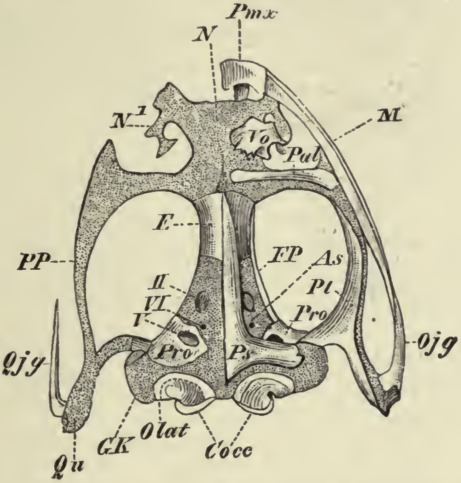


Fig. 611.—Frog skull from below. (From Wiedersheim.) For letters see fig. 612.

The cranium is increased by the addition of the large quadrate cartilage, which becomes applied to the otic capsule and (Anura) fuses with it, while the rest of its arch (pterygoquadrate) extends forward in a more or less complete condition, reaching the nasal capsule in the Anura. The quadrate cartilage is covered externally by the squamosal (paraquadrate), and supports the lower jaw, composed of Meckel's cartilage surrounded by membrane bones (dentary, splenial, angulare, etc.); its articular portion, like the quadrate, being rarely incompletely ossified. Vomers, palatines, and pterygoids appear in the base of the skull, all three forming a continuous arch in the Anura; in front of them lie the premaxillaries, and in most cases maxillaries. Between the hinder end of the maxillaries and the quadrate there may be a gap or it may be bridged by a jugal. By the modification of the quadrate into a suspensor the hyomandibular loses its function, and if represented at all, it is as part of the columella. The character of the remaining visceral skeleton depends upon the respiration (fig. 613). Where gills occur, the copula and hyoids—representing body and cornua—as well as four gill arches are present, but with pulmonary respiration the hyoid apparatus is reduced to a hyoid with anterior and posterior cornua, the gill arches being contained in the posterior horns.

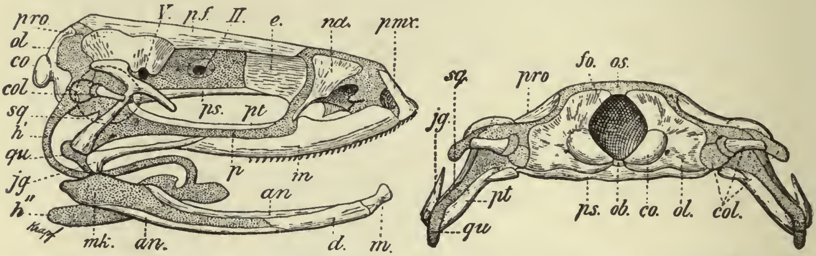


Fig. 612.—Lateral and hinder views of frog skull. (After Parker.) Letters for this and 611: *an*, angulare; *As*, alisphenoid cartilage; *co* (*Cocc*), occipital condyles; *col*, columella; *d*, dentary; *E* (*e*), sphenethmoid; *fo*, foramen magnum; *FP*, frontoparietal; *Gk*, otic capsule; *h′*, *h″*, hyoid and copula; *jg*, jugal; *M* (*m*), maxillary (in lower jaw mento-Meckelian); *mk*, Meckel's cartilage; *N*, *N*¹, nasal capsule; *na*, nasal; *ob*, *os*, cartilages from which basi- and supraoccipitals arise elsewhere; *ol* (*Olat*), exoccipital; *pf*, frontoparietal; *Pal*, palatine; *p* (*PP*), palatine arch; *Pmx*, premaxillary; *Pro*, prootic; *Ps*, parasphenoid; *Pt*, pterygoid; *Qu*, quadrate; *Qjg*, jugal; *sq*, squamosal; *Vo*, vomer. Cartilages dotted.

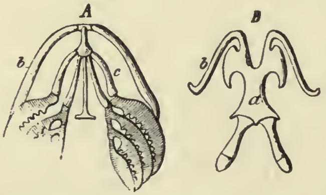


Fig. 613.—Hinder visceral skeleton of (*A*) larva of a salamander; (*B*) of toad. (From Gegenbaur.) *a*, body of hyoid; *b*, anterior horn (hyoid); *c*, rest of branchial skeleton.

With the assumption of a terrestrial life changes occur in the sense organs. The organs of the lateral line, which occur in all larvæ and are persistent in the aquatic perennibranchs, and the nerves which supply them, disappear; the eyes in the Salamandrina have upper and lower lids; in the frogs an under lid (really nictitating membrane). The nose becomes respiratory and is provided with choanæ opening into the mouth. Especially noteworthy is the auditory apparatus. This, in the urodeles and cæcilians, is very primitive, even the tympanum being absent, but in the Anura a sound-conducting apparatus appears. The spiracular cleft persists as a canal, opening into the pharynx by the Eustachian tube, its outer end expanded into the tympanic cavity and closed externally by the tympanic membrane, supported by the cartilaginous tympanic annulus (dotted circle in fig. 612, *B*). The connexion of the labyrinth with the tympanum is by an opening in the otic capsule, the fenestra ovalis, in which is the stapes (? part of capsule), the columella extending from this to the tympanic membrane and carrying the sound waves across to the inner ear. The brain (fig. 614) has advanced above that of the fishes in the stronger development of the cerebrum, but remains behind in the small size of the cerebellum, which is but a thin lamella.

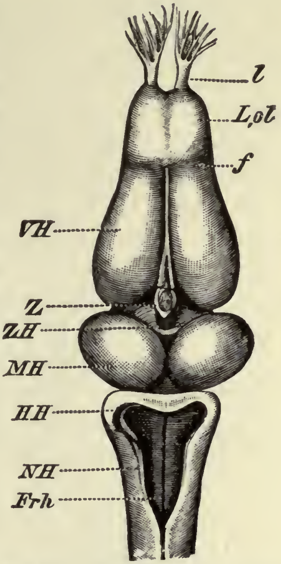


Fig. 614.—Brain of frog. *f*, line between olfactory lobes and cerebrum; *Frh*, fossa rhomboidalis; *HH*, cerebellum; *l*, olfactory nerve; *Lol*, olfactory lobes; *MH*, optic lobes; *VH*, cerebrum; *Z*, epiphysis; *ZH*, 'twixt brain.

The respiratory organs afford important characters, since both gills and lungs occur. Of gills there are two kinds, internal (found only in Anura), of entodermal origin, and ectodermal gills, external in position (figs. 4, 5), occurring in all. These ectodermal gills, three in number, are richly vascular and arise from the skin at the upper part of the gill clefts. The paired lungs open into the hinder part of the pharynx, either directly through the glottis or more rarely by a short trachea. Cartilages, the remnants of gill arches, may support trachea and glottis, and on the latter support vocal cords (larynx). Breathing is accomplished by a kind of swallowing, the air being forced into the lungs by the muscles of the floor of the mouth and the pharynx. Persistent gills and lungs are found only in the Perennibranchs. Usually the young breathe by gills, the adults by lungs, the origin of the metamorphosis to be described below.

Besides gills and lungs the skin is an important respiratory organ, as are pharynx and mouth cavity, in which the air must remain for some time on account of the respiratory mechanism. This renders intelligible the fact that many Salamandrina (*Spelerpes, Desmognathus, Plethodon, Gyrinophilus*, etc.) have neither gills nor lungs, but have only pharyngeal and cutaneous respiration. The capillary network in these parts is greatly developed and may extend into the epithelium. Thus, also, it happens that in the Anura the skin receives as large an artery as the lungs (fig. 616, *cu*).

The skin is thin and slimy from the numerous mucous glands, which not infrequently produce a poisonous secretion (so called parotid gland in the ear region). The epithelium bears a thin horny layer which at intervals is molted as a continuous sheet. The derma in the Anura is undermined by large lymph spaces, the presence of which makes the skinning of a frog such an easy matter. Ossifications in the skin—enormously developed in the fossil Stegocephali—occur but rarely (Gymnophiona) in recent Amphibia. On the other hand the abundance of chromatophores is noticeable, these, under the influence of the nerves, changing their shape and thus producing color changes in many Amphibia.

The heart (figs. 615, 616) has two auricles, distinctly separated in Anura, a right with venous blood, a left which with pulmonary respiration receives arterial blood. There is, however, but a single ventricle, and the arterial trunk is, at least externally, single. The arterial arches show different relations and have different fates. With branchial respiration the first three afferent and efferent arteries are connected in two ways, the one by the

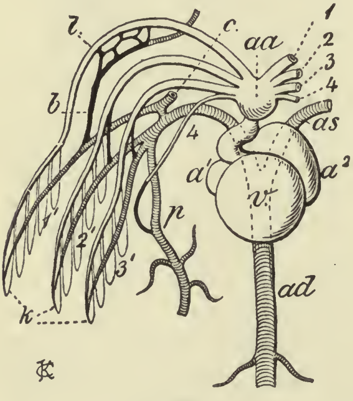


FIG. 615.

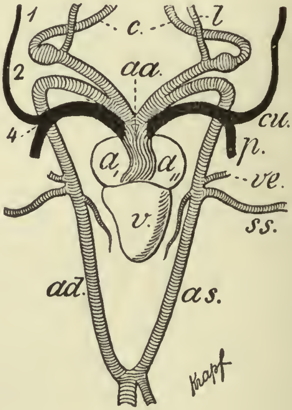


FIG. 616.

FIG. 615.—Heart and arterial arches of salamander larva. (After Boas.) a^1 a^2, right and left auricles; *aa*, arterial trunk; *ad*, dorsal aorta; *as*, left aortic arch; *b*, direct connexion between afferent and efferent arteries; *c*, carotid; *l*, afferent artery; *p*, pulmonary artery; *v*, ventricle; *1-4*, afferent arteries; *1'-3'*, gills.

FIG. 616.—Heart and arches of frog (diagram). $a_{,}$ $a_{,,}$, right and left auricles; *aa*, ventral aorta; *ad*, *as*, right and left aortic arches (radices aortæ); *c*, carotid; *cu*, cutaneus; *l*, lingualis; *p*, pulmonary artery; *ss*, subclavian; *v*, ventricle; *ve*, vertebralis; *1*, *2*, *4*, persisting arches.

capillaries of the gills, the other direct (fig. 615, *b*). In the fourth arch there is no gill system, but on the other hand this arch gives off the pulmonary arteries (*p*) to the lungs.

With the loss of gills (fig. 616) the third arch frequently disappears entirely (Anura), as well as the gill circulation of the others, while the direct circulation persists, at least in part. The first arch gives rise to the carotids, supplying the head (*c*); the second unites with its fellow of the opposite side to form the dorsal aorta; the fourth forms the pulmonary artery and, in the Anura, gives off a cutaneus artery (*cu*) to the skin. A longitudinal fold inside the arterial trunk is so arranged that the venous blood from the body coming to the heart through the right auricle is mostly sent out through the fourth arch to the lungs and the skin, while the blood returned from the lungs by the pulmonary vein passes through the left auricle and then through the first and second arches (carotid and aortic arches). So there is here a separation of pulmonary and systemic circulations, although the blood all passes through a common ventricle.

The sexual organs (fig. 581) are similar to those of selachians. The eggs pass from the ovary to the oviducts (Müller's duct), and in this are enveloped with a gelatinous layer. The spermatozoa, on the other hand, pass through the anterior part of the Wolffian body ('kidney') and thence out through the ureter. The distinction from the selachians lies in the fact that a urinary bladder, lying ventrally to the rectum, is present, at some distance from the urinary ducts, which open dorsally into the cloaca. Besides sexual organs fat bodies frequently occur, lobed and often brightly colored structures, best developed between the reproductive seasons.

A sort of copulation occurs, and internal impregnation is effected in many urodeles and in the Gymnophiona, but not in the Anura. The Anura and most other forms are oviparous, but occasionally, as *Salamandra maculosa* and *S. atra* of Europe, viviparous species occur. Many interesting brooding habits are known. The male of *Alytes obstetricans* wraps the cords of eggs about his legs and crawls into a hole until the young are hatched, while the females of *Amphiuma* and *Ichthyophis* watch over the eggs. The male of *Rhinoderma darwinii* has a large sac arising from the pharynx in which the eggs and young are cared for until the completion of the metamorphosis. In *Pipa americana* the male places the eggs on its back, the skin thickening around them so that each lies in a separate pocket, from which the young escape at length in nearly the adult form. In *Nototrema* and *Notodelphys* there are dermal sacs upon the back for the reception of the eggs.

The development of the Amphibia possesses special interest, since it affords the only easily observable instances of a metamorphosis among the vertebrates. This metamorphosis is the more marked the wider the adults are from the fishes. In the Anura a larva, the tadpole (fig. 4) escapes from the egg. It lacks lungs, but has three pairs of external gills, no legs, but a swimming tail with a fin-like fold. In the metamorphosis the gills and tail—larval organs—are lost, while lungs and legs are formed. A complication is introduced into the metamorphosis in that, for a time after the loss of the external gills, internal branchiæ, lying in gill slits, occur. These, however, are not visible from the exterior, since a fold of skin grows back over them, thus forming a cavity, the atrium, into which the gill slits open, and which in turn opens to the exterior by an opening (rarely paired), usually on the left side (fig. 617). In the tailed forms the metamorphosis is simplified, usually consisting in the loss of the external gills and sometimes in the change of form of the tail, which may lose its fin fold and become cylindrical. The last traces of a metamorphosis disappear in the perennibranchs, where lungs occur and the gills persist (*Siren* is said to lose the external gills and then re-form them). In the Anura the metamorphosis is lost when, as in *Hylodes martinicensis*, the whole development occurs in the egg, the young hatching in the adult form.

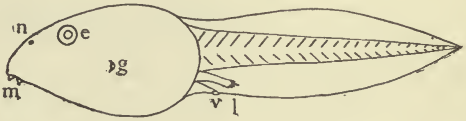


Fig. 617.—Side view of tadpole. *e*, **eye;** *g*, **opening of atrium;** *l*, **hind leg;** *m*, **mouth;** *v*, **vent.**

Order I. Stegocephali.

Extinct forms with well-developed tail, numerous membrane bones in the skull, and frequently a bony armor, at least on the ventral surface. Some were of gigantic size, and some from the folded condition of the enamel of the teeth are known as Labyrinthodonta. The group appears in the carboniferous (footprints in the Devonian), and died out in the trias.

Order II. Gymnophiona (Cæciliæ, Apoda).

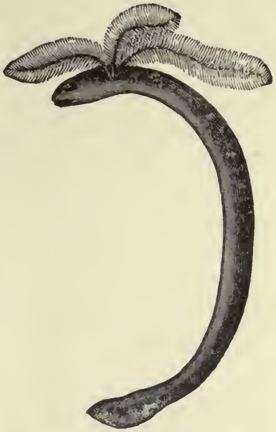


Fig. 618.—Larva of *Ichthyophis glutinosus*. (From Boas, after Sarasins.)

These are the nearest of living forms to the Stegocephali, but fossils are entirely unknown. The group is exclusively tropical, occurring in Ceylon, African islands, and America, a discontinuous distribution indicative of great age. They are burrowing animals and feed on small invertebrates. As a result of this subterranean life the eyes are small and concealed under the skin, the legs are entirely lost, so that the animals are snake-like in appearance. In the skin there are usually small bony scales; the drum of the ear is lacking; the vertebræ are amphicœlous. Inside the egg many species have three pairs of beautifully feathered gills (fig. 618), a proof of their pertinence to the Amphibia. Later, for a time, there is an external gill opening which finally closes. *Ichthyophis*, Ceylon; *Hypogeophis*, Seychelles; *Cœcilia*, America.

Order III. Urodela (Gradientia).

Of recent forms of Amphibia the urodeles are the most fish-like. The vertebral column consists of numerous vertebræ, and of these a large part are behind the sacrum and consequently belong to the tail. Ribs are present, but so short that they do not reach the sternum, which is weakly developed or is entirely absent. Tympanum, and Eustachian tube are entirely lacking, as are the vocal chords and the production of sound.

Sub Order I. PERENNIBRANCHIATA. Two or three gill slits, three bushy gills, and a swimming tail persist throughout life. *Necturus*,* mud puppy, with legs and two gill slits. *Siren*,* three gill slits, hind legs lacking. *Proteus*, of Austrian caves, much like *Necturus*, but nearly blind.

Sub Order II. DEROTREMA. External gills lost, but an opening in the neck leading to the gill slits. *Menopoma** (*Cryptobranchus*), hellbender, legs strong; *Amphiuma*,* legs rudimentary.

Sub Order III. SALAMANDRINA (Myctodera). After the loss of gills the gill slits close. *Amblystoma*,* remarkable for the length of time the larvæ retain their gills, *A. tigrinum* (fig. 5) and the Mexican axolotl even breeding in the larval stage. The adult of the true axolotl is unknown. *Plethodon*,* *Spelerpes*.* The European *Salamandra atra* and *S. macu-*

lata are viviparous, the former undergoing its metamorphosis inside the mother.

Order IV. Anura.

The anura have the compact bodies familiar in frogs and toads, with a small number (7–9) of trunk vertebræ and complete absence of tail; the caudal vertebræ being represented by a long bone, the urostyle. Ribs are sometimes distinct, sometimes fused to the transverse processes; the limbs are larger than in other Amphibia, and are frequently used for leaping and climbing. Ear drum and tympanic membrane are lacking only in the Pelobatidæ; their presence is correlated with the existence of vocal cords and the production of sound. The metamorphosis includes a tadpole stage.

Sub Order I. AGLOSSA. Toad-like anura with degenerate tongue and unpaired opening of the Eustachian tube. *Pipa* (p. 585), South America; *Dactylethra*, Africa.

Sub Order II. ARCIFERA. Tongue present, Eustachian tubes widely separate, coracoids of the two sides overlapping. BUFONIDÆ, toads, toothless; *Bufo*,* the dermal glands poisonous. PELOBATIDÆ, with teeth, usually no tympanum. *Scaphiopus*,* burrowing toad, with tympanum. HYLIDÆ, tree toads, toothed; tips of toes with sucking discs; *Hyla*,**Acris*.*

Sub Order III. FIRMISTERNIA. Tongue present, Eustachian tubes distinct, coracoids firmly united in the middle line. RANIDÆ, frogs. *Rana catesbiana*,* bull frog, the largest frog known; numerous other American species.

SERIES II. AMNIOTA.

Vertebrates with amnion and allantois (p. 554) in embryonic life; with the pro- and mesonephros functional only in the embryos, and replaced in the later stages by the true kidney (metanephros); ducts of the embryonic excretory system retained only so far as they have genital functions; gill slits appearing as transitory structures, but without gills and never functional. There are two great divisions of the Amniotes, the Sauropsida and the Mammalia. The Sauropsida include the Reptilia and the Aves, which agree with each other and differ from the mammals in having a single occipital condyle, the quadrate acting as suspensor of the jaws; ankle joint between the first and second rows of tarsals; the presence of epidermal scales, nucleated red blood corpuscles, and a cloaca.

Class I. Reptilia.

On account of similarity of form, the reptiles and Amphibia were long united. They form parallel groups: urodeles and lizards, frogs and turtles, cæcilians and snakes. Hence the points of distinction must be emphasized. The most important are two: the reptiles belong to the Amniota and, as such, have the embryonal features of the group; second, although often aquatic, they are, in the entire absence of branchial respiration, in character of skin and skeleton, in their entire structure, like the true land animals.

The skin, the better to withstand desiccation by the air, is strongly cornified, so that in the epidermis a many-layered stratum corneum and a many-layered stratum Malpighii can be distinguished. At the tips of the toes the stratum corneum develops strong claws. Further protection is afforded by the thick derma, often capable of being tanned into leather, in which not infrequently bony plates occur. Dermal glands are very rare, the femoral pores of the lizards (fig. 625, *b*), which appear like the ducts of glands, being produced by the ends of cornified epithelial cones. The axial skeleton, both skull and vertebral column, is nearly always ossified; only exceptionally (*Sphenodon* and the amphicœle Ascalabotæ) are considerable parts of the notochord retained. The vertebræ are usually procœlous.

In the skull of reptiles (as in the allied birds) are many characters which they share with Amphibia and which distinguish them from mammals. This is especially the case with the visceral skeleton. As in the Amphibia, the hinder end of the pterygoquadrate is attached to the otic capsule; the quadrate is ossified and affords the articulation for the lower jaw, which is composed of many bones. The squamosal lies at the base of the quadrate and, in the Squamata, is intercalated between it and the cranium. Behind it is the columella, its inner end inserted in the fenestra ovalis. From the quadrate the palatine series of bones—pterygoid, palatine, vomer—extends forward, these being frequently toothed; and in front of and parallel to it the pre-

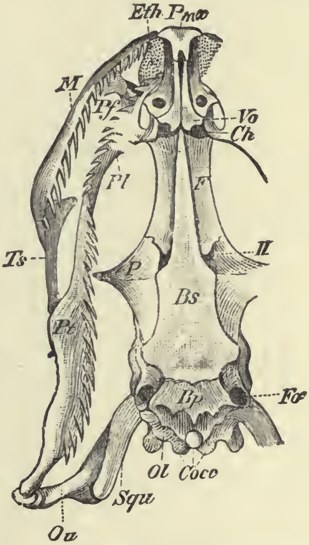


Fig. 619.—Ventral view of skull of *Tropidonotus*. (From Wiedersheim.) *Bp*, basioccipital; *Bs*, basisphenoid (in front also parasphenoid); *Ch*, choana; *Cocc*, occipital condyles; *Eth*, ethmoid cartilage; *F*, frontal; *Fo*, fenestra ovalis; *M*, maxillary; *ol*, exoccipital; *I*, parietal; *Pf*, prefrontal; *Pl*, palatine; *Pmx*, premaxillary; *Pt*, pterygoid; *Qu*, quadrate; *Squ*, squamosal; *Ts*, transversum; *Vo*, vomer; *II*, optic foramen.

maxillaries and maxillaries. Extremely characteristic of the reptiles, the turtles excepted, is an os transversum, which appears in no other vertebrates. It extends from the hinder end of the maxillary to the pterygoid (figs. 619, 626, 627, 630, *Ts*, *tr*). A jugal is also frequently present. Of the other visceral arches, since gills are lacking, only the hyoid bone and laryngeal cartilages persist.

In the cranium the complete ossification of the occipital region is noticeable, the four occipital bones being present. The basioccipital forms the larger part of the single occipital condyle, in which parts of the exoccipitals participate, the single condyle being the sharpest distinction between the reptilian and amphibian skull. The basisphenoid, which lies in front of the basioccipital, has an anterior process or rostrum, representing the rudimentary parasphenoid (possibly presphenoid). Above, the skull is roofed in with membrane bones: parietals (frequently fused and perforated by the parietal foramen for the pineal eye), frontals, nasals, as well as pre- and postfrontals and postorbitals, and usually lachrymals as well.

The ethmoidal region is largely cartilaginous; ali- and orbitosphenoids are small and variable. Only the prootic is constant in the otic region; epiotic and opisthotic usually fusing with the occipitals, the opisthotic being large and distinct only in the turtles. The zygomatic arch (lost in snakes) is formed of jugal and quadratojugal, while above it may be a second arch formed of postorbital and squamosal.

The convex occipital condyle forms, with the concave surface of the first vertebra (atlas), an articulation for motion in the vertical plane and lateral motions, while a twisting around the long axis of the body is permitted by the joint between the atlas and the second vertebra, the axis or epistropheus. The atlas is a bony ring, its centrum having separated and united with the body of the axis, forming a pivot around which the atlas turns. There are two sacral vertebræ, and the vertebræ of the trunk are divided into thoracic and lumbar, the former bearing long ribs which reach to the sternum, while the shorter ribs of the neck end freely.

Limbs are lacking in snakes and some lizards. When present the number of digits varies between three and five (usually four or five). In the pelvis ischium and pubis are separated by an obturator foramen and are united with the corresponding bones of the opposite side by a double symphysis. In the shoulder girdle scapula and coracoid alone are constant, a clavicle occurring in turtles and lizards, in the latter an episternum (fig. 564) as well. Of considerable systematic importance is the position of the ankle joint.

This is intertarsal in character, in that it occurs between the first and second rows of tarsal bones (fig. 636, *C*).

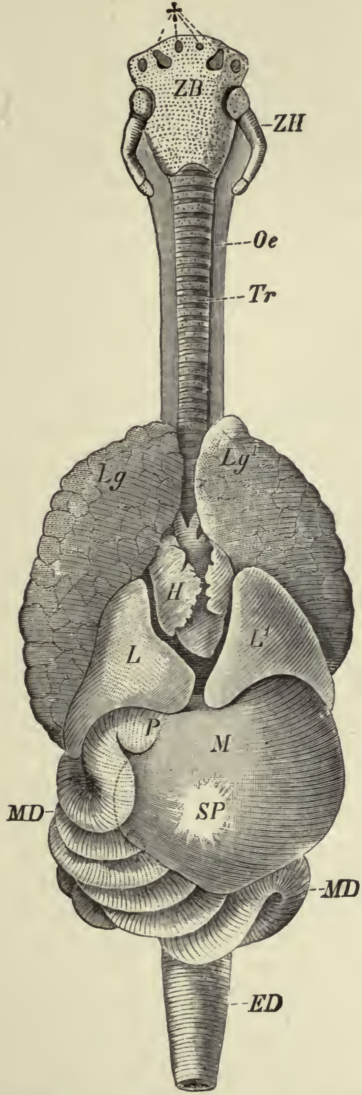


FIG. 620.—Viscera of Alligator. (From Wiedersheim.) *ED*, rectum; *H*, heart; *L*, liver; *Lg*, lung; *M*, stomach; *MD*, intestine; *Oe*, œsophagus; *P*, pylorus; *Tr*, trachea; *ZB*, body of hyoid; *ZH*, its cornua; *, perforations of hyoid.

Since reptiles lack even transitory gills, the gill slits are completely degenerate before the young escapes from the egg. Dermal respiration is far less important than with the Amphibia, lungs, as in birds and mammals, being the respiratory organs, and in these a progressive development may be followed. The larynx is followed by a trachea with cartilage supports in its wall, and this either opens directly into the two lungs or divides into two bronchi, which, in *Varanus,* may divide again inside the lungs. The lungs in the more primitive forms are subdivided only peripherally, but in the higher groups the whole is chambered, partitions extending inwards to the intrapulmonary bronchus.

Since the respiration is entirely pulmonary, the heart is divided into a left arterial and a right venous half, and a corresponding separation of systemic and pulmonary blood-vessels occurs (fig. 621). The two auricles are completely separated, while a septum extends into the ventricle, complete in the crocodiles, but not in turtles, lizards, and snakes. Yet even in the crocodiles a mixing of arterial and venous blood occurs since in the large aortic trunks which arise from both ventricles a communication, the foramen Panizzæ, persists. The arterial trunk is divided by internal partitions into three vessels, which are but rarely visible from the exterior. One of these arises from the right ventricle, carries venous blood, and takes over the fourth arterial arch, which gives off the pulmonary arteries (*4*, *p*). A second vessel arises from the right ventricle, is purely arterial and connects with most of the remaining arterial arches, the first, which gives off the carotid, and the right half (aortic arch, *ad*) of the second arch. The third vessel connects on the one hand with the remaining (left, second) arch and on the other with the right or venous half of the heart. The foramen Panizzæ occurs between this and the right aortic arch.

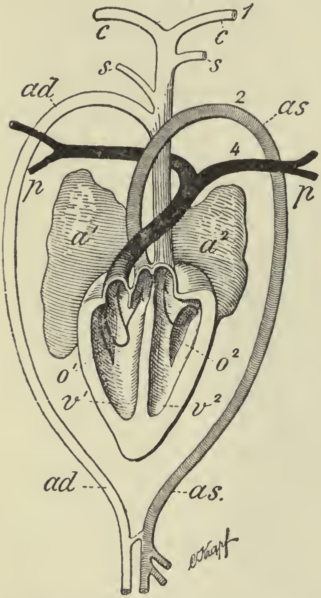


Fig. 621.—Heart of crocodile with arteries (diagram). a^1, a^2, right and left auricles; *ad*, *as*, right and left aortic arches; *c*, carotids; o^1, o^2, right and left auriculo-ventricular ostia; *p*, pulmonary artery; *s*, subclavians; v^1, v^2, right and left ventricles (the arrows show the direction of the blood flow); *1*, *2*, *4*, arches comparable with those of amphibia. Notice the origin of the vessels from the heart, and the connexion (foramen Panizzæ) between the arterial trunk and the left aortic arch, just in front of the heart.

The venous character of the left aortic arch and the incomplete ventricular septum (or presence of foramen Panizzæ) prevent a complete separation of systemic and pulmonary circulations. In the turtles a third element enters, the persistence of a ductus Botalli (as in Urodeles, fig. 580, *II, dB*).

To the foregoing adaptations to a terrestrial life may be added indications of higher development. The brain shows two advances. The cerebellum, especially in turtles and alligators, has become large, and the cerebrum grows dorsally and backwards over the 'twixt brain and forms the temporal lobes of the hemispheres. The parietal organ is developed as nowhere else. In many lizards it forms an unpaired dorsal eye lying beneath the skin in the parietal foramen. The paired eyes possess lids (usually upper and lower as well as a nictitating membrane), and frequently (turtles, lizards, and many fossils) a ring of bony plates (sclerotic bones) in the sclera. A new opening in the petrosal, the fenestra rotunda, places the tympanic cavity and the labyrinth in close relations.

In the excretory system amniote characters prevail. The Wolffian body with its duct is functional in the embryo. Later there arises behind it the permanent kidney (metanephros) with the ureter, while the embryonic structures disappear with the exception of those retained as accessory to the genital apparatus.

Thus in the male the vas deferens and epididymis are formed from the Wolffian duct; in the female the Müllerian duct (early lost in the male) becomes the oviduct. Usually the urogenital canals open dorsally in the cloaca, rarely in an elongation of the urinary bladder (Chelonia). This latter is lacking in snakes and crocodiles.

Almost all reptiles lay eggs; only in the Squamata (some snakes and lizards) are viviparous or ovoviviparous forms present. The eggs much resemble those of birds, in that the large yolk is surrounded with a layer of albumen and enclosed in a fibrous, often calcified shell. To open the egg the embryo has an egg tooth on the tip of the snout; this consists of dentine in the Squamata, but elsewhere, as in birds, is horny. From these relations it follows that internal impregnation must occur; the eggs undergo a discoidal (meroblastic) segmentation. Copulatory organs to accomplish this internal fertilization occur, and these are of classificatory importance, since they differ in character in the Squamata on the one hand, the turtles and crocodiles on the other. These differences are correlated with differences in the form of cloacal opening and in structure of skull and skin, so that all living species may be divided into two groups, the Lepidosauria, containing the lizards, snakes and *Sphenodon,* and the Hydrosauria with turtles and crocodiles. This, however, ignores the fossil forms. When these are taken into consideration another grouping must be adopted.

Order I. Theromorpha.

Extinct reptiles from the Permian and triassic which are closely related to the stegocephalous amphibia; with amphicœlous vertebræ, immovable quadrate, and from two to six sacral vertebræ. The ANOMODONTIA, with partial or complete loss of teeth, stand near the turtles, while the THERIODONTA, in which a heterodont dentition is developed, resemble in this and some other respects the mammals, which, by many, are supposed to have descended from them.

Order II. Plesiosauria.

Extinct aquatic forms from the triassic to the cretaceous, some forty feet in length. They had long necks, and the limbs were modified into swimming paddles recalling the flippers of the whales. The quadrate was immovable, and the jaws, with numerous teeth in sockets, were long.

Order III. Ichthyosauria.

These forms resembled the Plesiosaurs in skin, swimming feet, elongate jaws, and quadrate, but had the teeth (sometimes absent) in grooves rather than in sockets, and short necks. Some species at least were viviparous. Their range in time was like that of the preceding order.

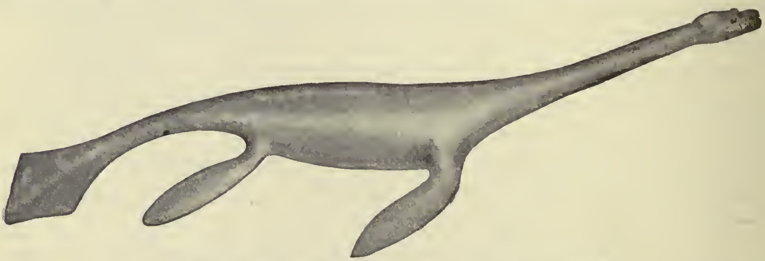


FIG. 622.—Restoration of *Plesiosaur.* (After Dames.)

Order IV. Chelonia (Testudinata).

The turtles form in external appearance a sharply circumscribed group, with the short and compact body enclosed in a bony case, from which only head, tail, and legs protrude (fig. 623). The case consists of a convex dorsal portion, the carapace and a flattened ventral plastron, the two being united in most forms at the margins. Each consists of bony plates, the positions and names of which may be learned from the adjacent cut. It only needs mention that the neural plates are united with the spinous processes, the costals with the ribs, and that the entoplastron is regarded as an episternum. It is not connected with the internal skeleton, since the sternum is lacking. The pelvis is only rarely fused with the plastron. This bony case is usually covered with horny shields, their number and arrangement usually agreeing with the plates of the case, although without their contours exactly coinciding.

More important are the great firmness of the skull and the immovable condition of the quadrate, the lack of an os transversum and of any but basisphenoid of the sphenoidal bones, and by growth forward, and backwards by which the girdles are brought inside the ribs. The teeth are entirely lost, and, as in birds, the jaws are enclosed in sharp horny beaks, in many cases efficient weapons against larger vertebrates. The cloacal opening is oval, its major axis corresponding to that of the body, and in its anterior end is an unpaired erectile penis used in copulation. Turtles appeared in the Permian, and the group has persisted until now.

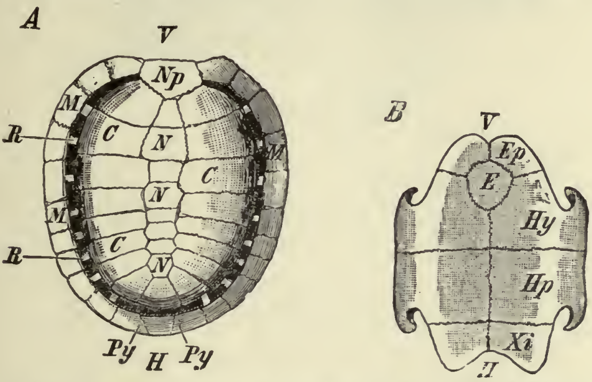


Fig. 623.—Carapace (*A*) and Plastron (*B*) of *Testudo græca*. (From Wiedersheim.) *C*, costal plates; *E*, entoplastron; *Ep*. epiplastron; *H*, posterior; *Hp*, hypoplastron; *Hy*, hyoplastron; *M*, marginal plates; *N*, neural plates; *Np*, nuchal plate; *Py*, pygal plate; *R*, ribs; *V*, anterior; *Xi*, xiphisternum.

Characters of armor and legs serve to contrast sharply the land and sea turtles; the first with well-developed legs, five-toed in front, four-toed behind, the toes with claws; the carapace arched, into which legs, head, and tail may be retracted. In the sea turtles the feet are flipper-like (fig. 624), claws mostly absent, and the carapace weakly united to or free from the plastron, flat and incapable of covering head or appendages. The fresh-water species are intermediate in position.

Sub Order I. ATHECA. Carapace of numerous mosaic scales and not connected with ribs and vertebræ; skin leathery. *Dermochelys* (*Sphargis*) *coriacea*,* the leather-back tortoise of warmer seas, reaches a weight of 1500 pounds.

Sub Order II. TRIONYCHIA. Fresh-water forms with poorly ossified carapace, but ribs and vertebræ connected with it. Our leather turtles (*Amyda* *) and soft-shelled turtles (*Aspidonectes* *) of savage habits belong here.

Sub Order III. CRYPTODIRA. Carapace well developed and united with ribs and vertebræ, but the pelvic arch free. The species are numerous, including terrestrial, fresh-water, and marine forms. CHELYDRIDÆ, fresh water, tail long. *Chelydra serpentina*,* snapping turtle; *Machrochelys lacertina*,* alligator turtle. CHELONIDÆ, marine, paddle-like feet. *Thalassochelys caretta*,* loggerhead; *Chelone mydas*,* green turtle, the favorite of epicures; *Eretmochelys imbricata*, whose horny shields furnish tortoise shell. TESTUDINIDÆ, terrestrial, including *Xerobates*,* the 'gopher turtle' of the South, the giant *Testudo* of the Galapagos Islands, and the enormous fossil *Colossochelys atlas* of India, 18–20 feet long, 8 feet high. Other families contain our mud turtles (*Kinosternon* *), box turtles (*Cistudo* *), and terrapins (*Malaclemmys* *).

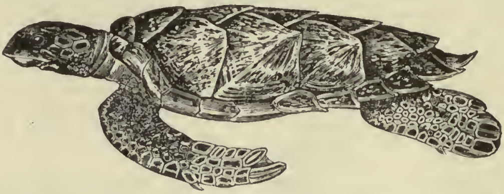


FIG. 624.—*Eretmochelys imbricata*, tortoise-shell turtle. (From Hajek.)

Sub Order IV. PLEURODIRA. Pelvis united to carapace and plastron. All belong to the southern hemisphere.

Order V. Rhynchocephalia.

These resemble the lizards not only in body form (four five-toed feet) and in scaly skin, but in certain anatomical matters as well: lack of hard palate, presence of epipterygoid, transverse cloacal opening, and heart, lungs, and brain. On the other hand they recall the crocodiles in having two postorbital arches and immovable quadrate. The large abdominal sternum and abdominal ribs are noticeable as well as the uncinate processes of the true ribs. The notochord is but incompletely replaced. The group appears in the Permian and is thus one of the oldest of reptilian types, and is usually regarded as ancestral to all the orders yet to be mentioned. The only living species, *Sphenodon* (*Hatteria*) *punctata*, belongs to the New Zealand region.

Order VI. Dinosauria.

This order included some of the largest land animals which have ever existed. Some of them were from forty to one hundred feet long and twelve to twenty feet high (*Amphicœlias*, *Camarasaurus*). In some there was an exoskeleton, some of the plates of which in the stegosaurs measured a yard across. Among the characters of the group are the fixed quadrate, jugal and postorbital arches, three to ten sacral vertebræ, and ilium elongate in front of and behind the acetabulum. Some of these forms (Orthopoda) in pneumaticity of bones, in having the pubic bones directed backwards, and in the formation of an intratarsal joint, resembled the birds, and have been regarded as the ancestors of that group. The Dinosaurs were confined to mesozoic time.

Order VII. Squamata (Lepidosauria, Plagiotremata).

One of the characters which unite lizards and snakes and which has given the name Plagiotremata is the transverse form of the cloacal opening (fig. 625), behind which, in the male, are the paired copulatory organs, each lying in a sac from which they can be everted like the finger of a glove. The names Squamata and Lepidosauria refer to the scaly condition of the skin. These scales are horny structures and somewhat distinct from the bony scales of fishes. The derma forms flattened papillæ which resemble the scales of fishes in that in many species they contain bony plates. These papillæ determine the character of the epidermis. Since the stratum corneum is especially thick on the top of the papillæ and thinner between them, rhomboid and oval plates occur, which either lie flush with each other (shields) or overlap like shingles (scales). The rule is that the head is covered with regularly arranged shields, each with its name, the trunk with scales in longitudinal, transverse, and oblique lines. Outside these is a layer of cornified cells, the pseudocuticula, and outside of all an inconspicuous true cuticle. Since all cornified cells are dead and

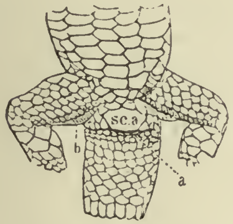


FIG. 625.

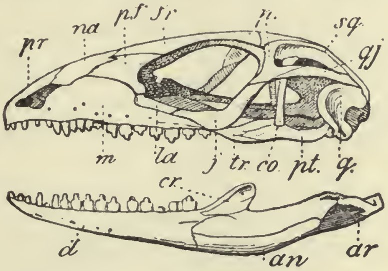


FIG. 626.

FIG. 625.—Hinder trunk and hind limbs of a lizard. (From Ludwig-Leunis.) *a*, cloacal slit; *b*, femoral pores; *sca*, anal shield.

FIG. 626.—Skull of *Ameiva vulgaris*. *an*, angulare; *ar*, articulare; *co*, epipterygoid; *cr*, coronoid; *d*, dentary; *fr*, frontal; *j*, jugal; *la*, lachrymal; *m*, maxillary; *na*, nasal; *p*, postorbital, above and behind it the parietal; *pf*, prefrontal; *pr*, premaxilla; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *tr*, transversum.

require periodic removal, the horny layers are cast yearly and replaced by new. During this periodic molting, which recalls that of arthropods, the animals are sickly and apt to die in captivity.

All Squamata are characterized by the slenderness of the cranial bones (fig. 619, 626, 627), which, especially in the Lacertilia, incompletely close in the cranium. The quadrate is movable. and the squamosal is intercalated between it and the cranium. A hard palate is lacking, and the choanæ, as in the amphibia, lie far forward (fig. 619, *Ch*). There is a wide gap in the partition between the two ventricles of the heart.

Sub Order I. LACERTILIA (Saurii). The lizards are usually distinguished from the snakes by the possession of limbs, but a few forms, undoubted lizards, like the glass snakes and Amphisbænæ, lack limbs. These are distinguished by the existence of the scapula and the iliac bone united to the vertebra, and especially by the presence of a sternum, which never occurs in snakes. In the skull is a peculiar bone (lacking only in Chameleons and Amphisbænæ), found nowhere else, the epipterygoid (fig. 626, *co*); it reaches from the pterygoid to the parietal, and from its slender shape is sometimes called columella, but is not to be confounded with the true columella of the ear. The bones of the jaws are firmly united, so that the mouth has no special capacity for opening widely. The jugal-quadratojugal arch is present.

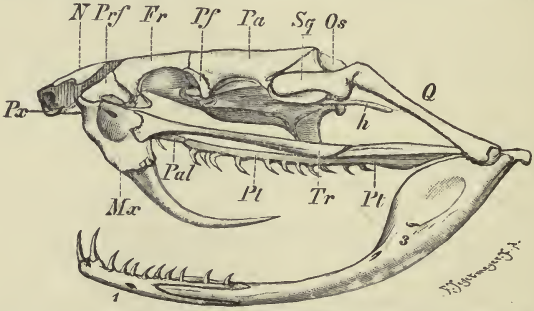


FIG. 627.—Skull of rattlesnake. (From Boas.) *Fr*, frontal; *h*, hyomandibular (columella); *Mx*, maxillary: *N*, nasal; *Os*, supraoccipital; *Pa*, parietal; *Pal*, palatine; *Pf*, postfrontal; *Prf*, prefrontal; *Pt*, pterygoid; *Px*, premaxilla; *Q*, quadrate; *Sq*, squamosal; *Tr*, transversum; *1*, dentary; *3*, articulare.

In external appearance the presence of eyelids, nictitating membrane, tympanic membrane, and Eustachian tube are noticeable, these being absent only in the Amphisbænæ. In the Ascalabotæ, as in snakes, the lids grow together, forming a transparent covering over the eyes. Fossil lizards are rare, but the group dates back to the cretaceous.

Section I. ASCALABOTÆ (geckos). Skeleton incompletely ossified, notochord persistent, amphicœle vertebræ; skin granular rather than scaly, usually adhesive discs on the toes by which they climb vertical surfaces or can walk upon ceilings. Two hundred species. *Phyllodactylus*.*

Section II. CRASSILINGUIA. Tongue thick, fleshy, not protrusible from the mouth, or only slightly so. IGUANIDÆ; American, often a comb of spines on the back, teeth pleurodont, *i.e.*, firmly united to the inner side of the jaw. Three hundred species. *Anolis*,* *Sceleporus*,* *Phrynosoma*,* 'horned toads.' AGAMIDÆ; Old World, teeth acrodont, *i.e.*, seated on the angle of the jaw bones. One hundred and fifty species. *Chlamydosaurus*, *Draco volans*, with ribs greatly elongate and supporting a dermal fold which acts as a parachute.

Section III. FISSILINGUIA. Tongue long and thin, divided at the tip, and capable of wide protrusion from the mouth, and in *Varanus* retractile into a sheath. TEJIDÆ; American, teeth acrodont; *Cnemidophorus*,* *Tejus*. HELODERMATIDÆ, pleurodont; *Heloderma*,* the 'Gila monsters,' are the only poisonous lizards. LACERTILIDÆ (*Lacerta*) and VARANIDÆ (*Varanus*, the monitors) are Old World forms, *Lacerta vivipara* bringing forth living young.

Section IV. BREVILINGUIA. Tongue short, slightly notched at the tip, slightly protrusible. Four hundred species. SCINCIDÆ, with tendency to reduction of the limbs. *Eumeces*,* *Oligosoma*.* In *Anguis* and *Typhline* the legs are absent. ZONURIDÆ, with a finely scaled groove along the side; all Old World except our *Ophisaurus ventralis*,* the glass snake, a limbless form with brittle tail.

Section V. ANNULATA. In many respects snake-like; legs and epipterygoid, tympanum, and movable eyelids lacking and usually girdles; tropical or subtropical. In *Chirotes* sternum and reduced fore legs retained. *Amphisbœna*.

Section VI. VERMILINGUIA; includes the Old World chameleons (our 'chameleon' is *Anolis*,—*supra*) with long fleshy tongue, lying rolled up in the mouth, but protrusible and used for catching insects, its end being covered with a sticky mucus. Other characteristics are the ring-like eyelids functioning as an iris, the climbing feet in which the toes are united into two opposable groups; epipterygoids, clavicle, sternum, and tympanic membrane lacking. The chameleons are best known from their changes of color, produced by rapid alterations in the size and shapes of the chromatophores. Color changes occur in other lizards, but not to such an extent as here.

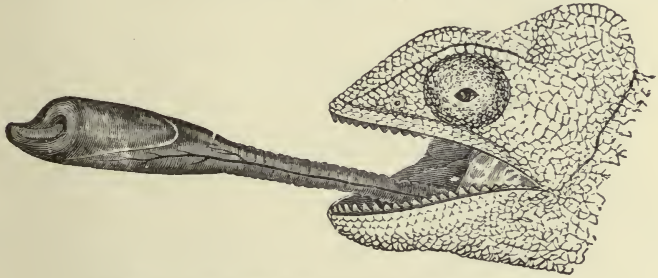


FIG. 628.—Head of chameleon with tongue extended.

Sub Order II. PYTHONOMORPHA. Large, extinct, extremely elongate reptiles with four flipper-like limbs and strong swimming tail. Flourished in the cretaceous. *Mosasaurus*, *Clidastes*.

Sub Order III. OPHIDIA. The snakes are distinguished from most lizards by the absence of limbs, and connected with this the similar vertebræ in which only trunk and caudals can be distinguished. The caudals lack ribs, but these are present and long in the trunk region, serving for locomotion and supporting the body on their distal ends. Since there are legless lizards, it is further necessary to say that in the Ophidia the girdles and sternum are lost, only the Peropoda having remnants of the hinder appendages and pelvis, but these not connected with the vertebral column.

Further distinctions exist in sense organs and jaws. The columella is indeed present, but tympanum and Eustachian tube are lacking. The eyelids also seem to be wanting, but examination shows, in front of the cornea and separated from it by a lachrymal sac, a transparent membrane, composed of the fused eyelids (outer cornea). The apparatus of the jaws (figs. 619, 627) is remarkable for its great extensibility, which enables snakes to swallow animals larger than themselves, after coiling around them and crushing them. This extensibility is in part due to the fact that the bones of the lower jaw are bound together at the symphysis by elastic ligaments, in part to the freedom of motion of the bones of the upper jaw (excepting the small premaxillaries) and the palate. Further, the squamosal (*Sq*), quadrate (*Q*), and transversum (*Tr*) are elongate and slender, the quadrate being widely separated by the squamosal from the skull, while the zygomatic arch is entirely absent. The food is forced down the throat by hook-shaped bones on palatines and pterygoids. A wide distension of the stomach is rendered possible by the elasticity of its walls and the great mobility of the ribs, which are not united ventrally by a sternum.

In the non-poisonous snakes the dentition is similar on jaws and palate bones (fig. 619). The vomer and, usually, the premaxilla are toothless. In the poisonous serpents poison fangs appear on the maxilla (fig. 627) and are distinguished from the other teeth by their greater size and connexion with a large poison gland. The duct of the gland opens at the base of the tooth; the poison which is pressed out by the pressure of the jaw muscles is led to the tip of the tooth either by a groove (proteroglyphic tooth, fig. 629, *A*) or, when the groove is closed to a canal (solenoglyphic tooth, *B*), through this canal which opens at base and tip of the tooth.

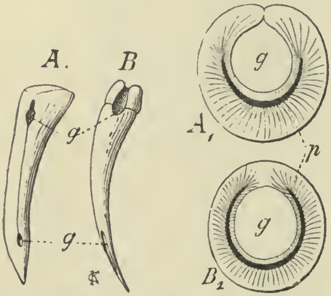


FIG. 629.—Poison fangs. *A*, A_1, proteroglyphic (grooved) tooth of cobra, and section of same; *B*, B_1, solenoglyphic tooth (tubular) of rattlesnake; *g*, poison canal; *p*, pulp cavity.

The asymmetrical character of the lungs is interesting. In the Peropoda one lung (apparently the left) is much smaller than the other; in the poison snakes and some others it is rudimentary or even absent. In the Typhlophidæ, on the other hand, the right appears to be degenerate. The urinary bladder is always absent. The excreta, chiefly uric acid, accumulate as a solid mass in the cloaca and form the chief part of the excrement; the fæces, on account of the extraordinary digestive powers, being small in amount.

Section I. OPOTERODONTA (Angiostoma). Burrowing blind tropical snakes with the mouth incapable of distension, the animals living on small insects. *Typhlops.*

Section II. PEROPODA. These large snakes have paired lungs and rudiments of hind extremities; lack poison fangs, and kill their prey by muscular power. *Python*, Africa; *Boa* and *Eunectes* (anaconda), South America.

Section III. COLUBRIFORMIA. Ordinary snakes (over 500 species) with numerous teeth in the upper jaw, but with appendages entirely absent. Some are poisonous, some not, but no structural lines can be drawn between them. The AGLYPHA have no grooved teeth. *Tropidonotus*,* water snakes; *Bascanion*,* black snakes; *Eutainia*,* garter snakes. The PROTEROGLYPHA, with grooved teeth, permanently erect, are poisonous. Most are brightly colored. *Elaps*,* the coral snake; *Naja tripudians*, the cobra of India; *N. haje*, Cleopatra's asp. Here belong the pelagic sea snakes of the Indo-Pacific, which are viviparous.

Section IV. SOLENOGLYPHA. With the maxilla reduced and serving as a socket for the single large tubular tooth with one or more reserve teeth (fig. 627). VIPERIDÆ, Old World, no pit between nostril and eye. CROTALIDÆ, New World and Asia, with a pit between nose and eye. *Crotalus*,* with the tail ending in a rattle formed by remnants of cast skins, is common throughout the United States. *Agkistrodon contortrix*,* copperhead, and *A. piscivorus*, moccasin, lack the rattle. *Bothrops lanceolatus* of the Antilles, possibly the most poisonous snake.

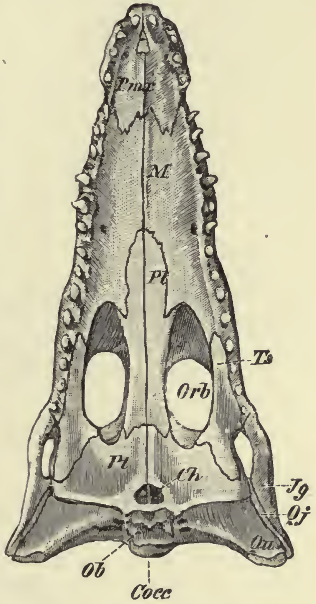


FIG. 630.—Ventral surface of skull of crocodile. (From Wiedersheim.) *Cocc*, occipital condyle: *Ch*, choana; *jg*, jugal; *M*, maxillary; *Ob*, basioccipital; *Orb*, orbit; *Qi*, quadratojugal; *Qu*, quadrate; *Pl*, palatine; *Pmx*, premaxilla; *Pt*, pterygoid; *Ts*, transversum.

Order VIII. Crocodilia (Loricata).

The crocodiles, alligators, etc., agree with some of the forms already mentioned in the oval cloacal opening with single copulatory organ, immovable quadrate, and the bony plates in the skin. In shape they are lizard-like, but in structure they differ from all other living reptiles and approach most nearly to the Theromorphs. The maxillaries, palatines, and pterygoids have united in the living species in the middle line, forming a hard palate and forcing the vomers upwards into the nasal region. This same process has carried the choana (fig. 630, *Ch*) to the back of the skull. Some of the ribs have two heads; the ears and nostrils are provided with valves. A sternum is present and, farther back, abdominal ribs and an abdominal sternum. The jaws are extended into a long snout, and the teeth, which occur only on the margins, are placed in sockets (alveoli). The four-chambered heart has already been described (p. 592). The animals move slowly on land, but in the water, thanks to their strong, keeled tail, they are very active. They have a strong smell, owing to musk glands in the cloaca and on the under jaw. The group appeared in the trias, and of the three sub orders two, the Pseudosuchia and Parasuchia, are extinct.

Sub Order EUSUCHIA. External nostrils united, choana posterior; five toes in front, four behind. *Gavialis*, India, snout long and slender. *Alligator lucius*,* alligator; *Crocodilus*,* most species Old World, one, *C. americanus*,* occurring in our southern waters.

Order IX. Pterodactylia (Pterosauria).

Extinct reptiles of the Jurassic and cretaceous, adapted for flight. The bones were hollow and the wings were broad membranes, supported, like those of a bat, by the body and the greatly elongated fifth digit of the fore limbs. Some were sparrow-like in size and some, *Pteranodon*, had a wing expanse of twenty feet. Yet one of these large forms from Kansas had its pelvic opening so small that its eggs could not have been more than half an inch in diameter.

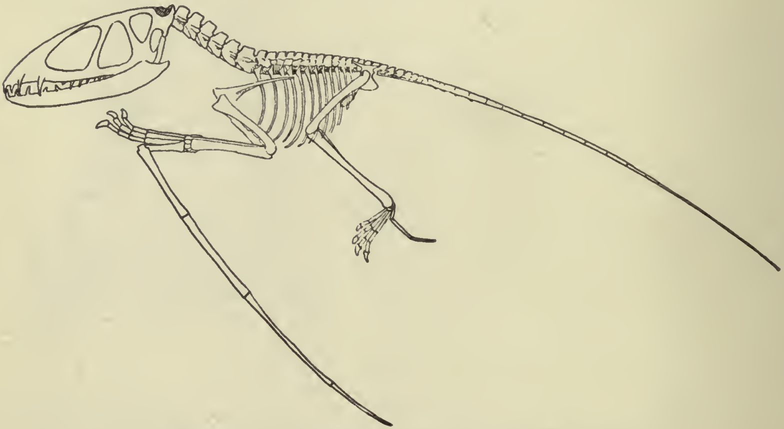


FIG. 631.—*Dimorphodon*, a pterodactyle. (After Woodward.)

Class II. Aves.

While structurally the birds stand very near the reptiles, yet by the development of wings and the feathering of the body the group is one strictly circumscribed. The skin is in some places, as the lower part of the legs, covered with horny scales and shields, on the toes are claws, but as a rule the fingers are feathered. On most places the skin is soft and thin, since the derma and stratum corneum are poorly developed. Periodic molts of the integument do not occur, since the horny layer, as in mammals, undergoes a constant renewal. These peculiarities of the skin are correlated with the appearance of the protecting plumage.

The feather, like the hair of mammals, is exclusively epithelial in character, but of a much more complicated structure. The cornified epithelium forms a firm axis, the scape, from which, right and left, arise branches, or barbs. The scape is solid as far as the barbs extend (rachis, or shaft), while below it is hollow (quill, or calamus). The quill is inserted deep in the derma, in a follicle, and is provided with muscles for its movement. Its hollow in most fully developed feathers is empty save for the 'pith,' a small amount of dried tissue. In young growing feathers it is occupied by a richly vascular connective tissue, the feather papilla, which, for purposes of nourishment, extends inwards from the derma. The feather may therefore be regarded as a cornified outgrowth from the skin which has arisen on a papilla of the derma, a view which corresponds well with its development and shows its homology with the scales. In many birds (cassowaries) two well-developed feathers arise from the same follicle—a fact which explains the existence of a rudimentary feather, the hyporachis, or after-shaft, attached to the scape below.

In contour feathers the barbs are, to a great extent, united into a vane. Right and left of the shaft they lie close together and parallel, each repeating in miniature the entire feather, the barb having branches or barbules, which, overlapping the barbules of adjacent barbs, give the vane its close texture. The vane is held together by minute hooks on the barbules of one barb interlocking with those of the next. Down feathers (plumes) differ from contour feathers in the absence of hooks and the loose arrangement of the barbs. Since feathers consist of cornified epithelium and these cells are held firmly (only in powder down is there a gradual loss), they, like the scaly coat of the snakes and lizards, must be molted yearly and replaced by new.

Young birds or embryos have only down feathers. Later the contour feathers arise in regular order in the feather tracts, or pterylæ, between which are apteria in which no contour feathers appear (fig. 632). Since the contour feathers overlap like shingles, they form a firm coat of plumage beneath which the down and semiplumes form a warm coat.

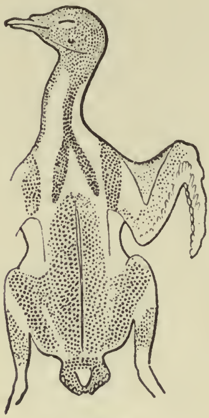


FIG. 632.

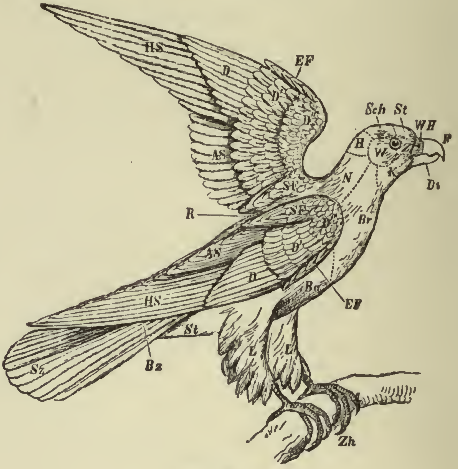


FIG. 633.

FIG. 632.—Feather tracts and apteria of pigeon, dorsal view. (From Ludwig-Leunis.)
FIG. 633.—Regions and feathers of *Falco lanarius*. (From Schmarda.) *As*, secondaries; *Ba*, belly; *Br*, breast; *Bz*, rump; *D'*-*D'''*, wing coverts; *Di*, gonys of bill; *EF*, alula; *F*, culmen of bill; *H*, occiput; *HS*, primaries; *K*, throat; *L*, legs; *N*, neck; *Sch*, crown; *SF*, parapterium; *St*, forehead, lower tail coverts; *Sz*, rectrices; *W*, cheek; *WH*, cere with nostril; *Zh*, toes.

Besides these covering feathers (coverts, or tectrices, fig. 633, *D*) there are the longer feathers of the wing, the remiges, and the tail feathers, or rectrices (*Sz*). The larger remiges form the chief part of the wing; they spring from the part of the limb corresponding to the hand (carpus, metacarpus, phalanges) and are known as primaries (*HS*), while the secondaries (*As*), arising from the forearm, are shorter. These are overlapped at the base by the coverts (*D*, *D'*, *D''*) and by the parapterium (*SF*) springing from the shoulder. A few feathers arising from the first finger remain distinct from the remiges and form the alula (*EF*). In the water birds especially the feathers are oiled by the secretion of a pair of glands at the base of the tail above the coccyx.

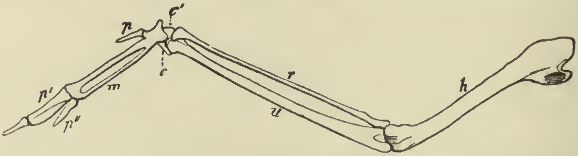


FIG. 634.—Wing skeleton of stork. (From Gegenbaur.) *c*, *c'*, carpalia of first row; *h*, humerus; *m*, fused metacarpals and carpals of second row; *p*-*p''*, phalanges of first three fingers; *r*, radius; *u*, ulna.

Since the feathers are not only for protection, but give to most birds the power of prolonged flight, they predicate a special mode of life, under the influence of which all of the other organs exist. The character of the skeleton, the respiratory organs, and in part the sense organs and brain, are connected with the powers of flight.

As the feathers of the wings, like the fins, form what may be called a paddle working as a whole, the skeleton of these limbs is simplified (fig. 634), first, by the reduction of the fingers, of which only three with a small number of phalanges persist (p, p', p''); second, by fusion of the corresponding metacarpals (m) with each other and with the adjacent carpal bones. On the other hand, in order that there may be the necessary energy and the most complete transfer of the same to the body, the connexion with the skeletal axis is strengthened by special development of the parts. In the shoulder girdle (fig. 635) all three elements are firm, a sword-shaped scapula (*s*), a columnar coracoid (*c*), and clavicles which are usually united to a 'wish-bone,' or furcula (*f*). Clavicles and furcula are united directly or by ligaments to the broad sternum, the anterior face of which is developed into a strong keel, the carina, or crista sterni, in order to give the largest surface for attachment of the large muscles of flight. Usually the greater the powers of flight the more developed the carina, yet in some cases (albatross) the weak carina is compensated for by the enormous width of the sternal plate. In running birds (ostriches, etc.) the carina is entirely gone. The thoracic framework is rendered more firm by the development of uncinate processes from the vertebral parts of the ribs (*u*) which overlap the succeeding ribs.

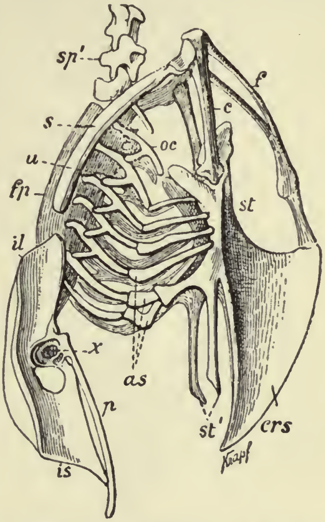


FIG. 635.—Trunk skeleton of stork. (From Gegenbaur.) *as*, sternal part of rib ; *c*, coracoid ; *crs*, keel ; *f*, furcula (fused clavicles) ; *fp*, fused spinous processes of thoracic vertebræ; *il*, ilium; *is*, ischium; *oc*, vertebral part of ribs; *p*, pubis; *s*, scapula; *sp*. spinous process; *st*, *st'*, sternum and abdominal processes; *u*, uncinate processes; *x*, acetabulum.

Since the fore limbs are no longer used for walking, the support of the body depends upon the hinder extremities, and this has brought about two striking characteristics—the broad union of the pelvis with the vertebral column, and the simplification of the leg skeleton. In the embryo the ilium (fig. 635, *il*) is connected only with the two sacral vertebræ present in most reptiles, but later it extends forward and back, uniting with at least nine vertebræ and sometimes with as many as twenty-three; while the iliac bones of the two sides meet dorsal to the vertebral column. This extensive union of pelvis and axial skeleton is understood when we recall that in walking or at rest the vertebral column is not vertical as in man, but is inclined. Ischium and pubis are peculiar in that they extend backwards, parallel to each other, from the acetabulum, and that only exceptionally (ostrich) are the bones of the two sides united by a symphysis.

In the hind limbs occur conditions similar to those which will be repeated in the ungulates. The weight of the body makes it necessary that the simplification found in the wing should be repeated in the lower leg and foot, and that the numerous bones usually occurring in these regions be replaced by one which shall support the pressure (fig. 636). Therefore the fibula, well developed in the embryo (*B*), becomes reduced to an inconspicuous rudiment; the metatarsals, distinct in the embryo (*B*), fuse to a

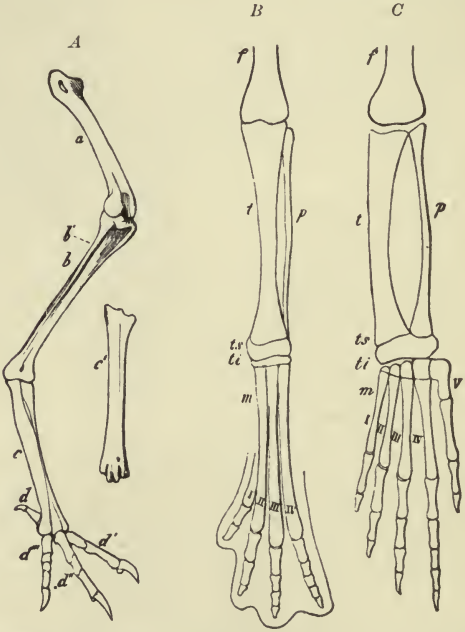


FIG. 636.—*A*, leg of *Buteo vulgaris*. *a*, femur; *b*, tibio-tarsus; *b′*, remains of fibula; *c*, tarso-metatarsus; *c′*, same, front view; d^1–d^3, toes. *B*, lower leg of bird embryo; *C*, of lizard. *f*, femur; *t*, tibia; *p*, fibula; *ts*, tarsales of first row (talus); *ti*, tarsales of second row; between these intertarsal joint; *I–V*, digits. (From Gegenbaur.)

single tarso-metatarsus (*A*, *c*), which has below as many articular surfaces as there are toes (since the fifth toe only appears in the embryo, at most four, in some three or even two, *d*–*d'''*). At the same time the tarsals disappear by fusion with adjacent parts. Even in reptiles (*C*) a part of the tarsals unite with the bones of the shank, and the remainder with the metatarsals; in the birds the union is completed, the proximal series fusing with the lower end of the tibia to form a tibio-tarsus, the distal with the metacarpus to form the tarso-metatarsus, in this way producing the intertarsal joint so characteristic of birds.

In respect to the vertebral column, it only needs mention that the vertebræ articulate with each other by a so-called saddle-joint, that (in living birds) only a few caudal vertebræ persist behind the pelvis, that these are partially fused to a single bone, the pygostyle, which supports the tail feathers, and that, corresponding to the well-developed neck, there are many cervical vertebræ, among them an atlas and an axis, all except the last two fused with the corresponding cervical ribs.

The skull (fig. 637) resembles closely that of the lizards in the presence of a single occipital condyle, in the movable condition of the quadrate upon the cranium, and in the presence of a slender columella. On the other hand an os transversum is lacking. The cranium, as a result of the increase in size of the brain, is more spacious; the bones of its walls fusing early so that the sutures between them are obliterated. The occipital condyle is on the under surface, so that the skull is carried at nearly right angles to the axis of the vertebral column. Teeth are lacking in living birds, although they occurred in some fossil forms. In their place

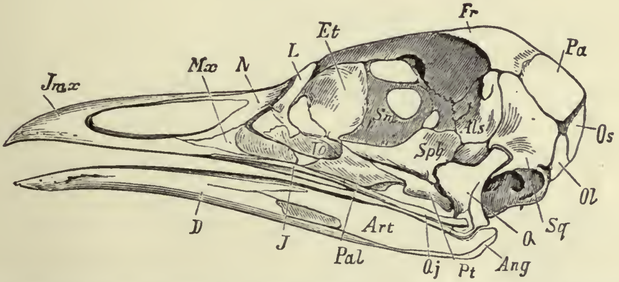


Fig. 637.—Skull of young bustard. (From Claus.) *Als*, alisphenoid; *Ang*, angulare; *Art*, articulare; *D*, dentary; *Et*, mesethmoid; *Fr*, frontal; *Jmx*, premaxillary; *J*, jugal; *L*, lachrymal; *Mx*, maxillary; *N*, nasal; *Ol*, exoccipital; *Os*, supraoccipital; *Pa*, parietal; *Pal*, palatine; *Pt*, pterygoid; *Q*, quadrate; *Qj*, quadratojugal; *Sm*, interorbital septum; *Spb*, basi- and presphenoid.

are hard horny sheaths covering the jaws which are frequently carried back on the outside into a softer cere (fig. 634, *WH*).

The cranium consists of four occipitals, a basi- and a presphenoid; above, the parietals and frontals; and on the sides prootics, alisphenoids and orbitosphenoids, while the broad squamosals also enter its wall. The large mesethmoid lies in the interorbital septum; the nasal cavity is roofed by the nasals, and beside them are the lachrymals. The quadrate articulates with the squamosal, and from it extend forward internally the pterygoid, palatine, and vomer; externally a zygomatic arch of quadratojugal and jugal to the maxillaries and premaxillaries. The maxillaries are hinged in the ethmoidal region, so that in opening the mouth there is besides the depression of the lower jaw an upward motion of the upper jaw.

The pneumaticity of the bones is an important feature of the skeleton. In place of marrow and bony tissue, the inside of the bones in strong flying birds is more or less completely occupied by air spaces, around which, as a sheath, is the compact bone. This gives the greatest possible lightness and strength to the skeleton. In *Buceros* and *Palamedea* all of the bones are pneumatic; in others (*Pelecanus*, *Sula*, *Tachypetes*, etc.) only the phalanges of the toes contain marrow, while in the penguin and *Apteryx*, as in mammals, air spaces occur only in some of the cranial bones.

The air spaces of the bones are in part (skull) connected with the nose and tympanum, but most of them, by means of the air sacs, communicate with the lungs. The long trachea forks at its lower end into two bronchi. At its upper end is a larynx, as in other vertebrates, but this is not vocal; the notes of birds are produced by the syrinx, which lies at the division of trachea into bronchi. It is usually formed of both trachea and bronchi, but more rarely of either trachea or bronchi alone. Its vocal cords are regulated by special muscles, which in the singing birds have a complicated arrangement. The relatively small lungs send out from their surface air sacs, especially well seen in embryos (fig. 638, *1–5*). These later become large, thin-walled spaces, easily torn away in dissection, leaving large openings on the surface of the lungs (fig. 639, *1–5*). Usually five pairs of these air sacs are present, largely in the cœlom, but extending in between the muscles (breast and axillary region), and also into the bones.

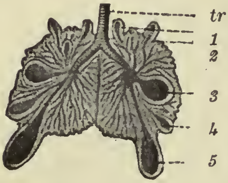


FIG. 638. — Development of trachea, lungs, and lung sacs of a chick. (After Selenka.) *tr*, trachea; *1–5*, lung sacs.

The spongy lungs lie on either side of the vertebral column and are united to the ribs. On entrance to the lung the bronchus (fig. 639, *br*) loses its cartilage supports and enlarges into a vestibule (*v*) and extends thence as a mesobronchus (*bm*) backwards, terminating in the abdominal air sac (*5*). A side branch supplies the hinder subcostal sac (*4*). Secondary bronchi arise from the vestibule and mesobronchus; of these there are three to five entobronchi (*I–IV*) supplying the remaining air-sacs and six or more ectobronchi. Arising from the mesobronchi and secondary bronchi are tertiary bronchi, or air pipes, running parallel to each other and anastomosing frequently. Each air pipe has a thick spongy wall (fig. 640) composed of numerous thin-walled sacs, the lung vesicles, closely enveloped by capillaries, and connected with the central air-conducting tube, the lumen of the pipe.

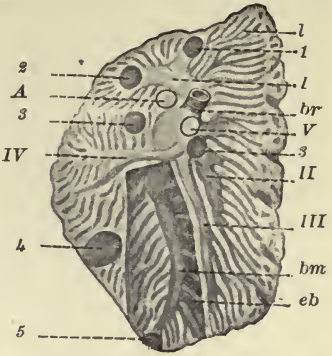


FIG. 639.—Right lung of hen, somewhat diagrammatic. A window shows a mesobronchus with its branches. *a*, artery; *bm*, mesobronchus, arising from the vestibule: *br*, bronchus swelling to vestibule; *eb*, ectobronchus; *l*, lung pipes; *I–IV*, mesobronchi; *1–5*, ducts of lung sacs.

Inspiration is effected by raising the framework of the chest, this causing a straightening of the hinged ribs and an increase of the sterno-vertebral diameter; expiration by the reverse motion. By this the lungs, attached to the ribs, are alternately enlarged and contracted in spite of their slight elasticity. This is also true of the lung sacs, which, on account of their poor blood supply, are not respiratory but serve as accessory air pumps. It is probable that in flight this air-pump action occurs especially with the subpectoral and axillary air sacs, drawing air through the lungs and rendering other respiratory motions superfluous, thus enabling the thorax to remain quiet, an important matter. If the trachea be closed and the air canal in the humerus opened, the bird can breathe through the latter.

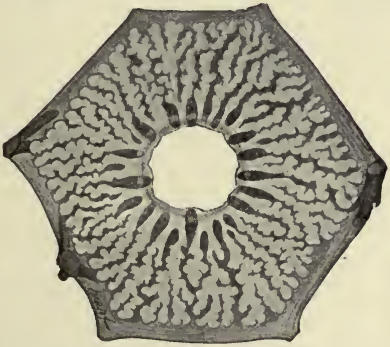


FIG. 640.—Section of lung pipe. (After Schulze.)

The circulation in the birds has arisen from that of the reptiles by complete separation of systemic and pulmonary systems. Of the three great arterial trunks present there (fig. 621), the pulmonary artery and the right aortic arch, arising from the left ventricle, are retained, the left venous arch being lost. The septum between the ventricles is complete. The striking features of the alimentary canal (fig. 60) are the crop (not always present), a glandular stomach or proventriculus (*c*), and a muscular chewing stomach or gizzard (*d*), as well as two long, rarely rudimentary, cæca (*k*) at the junction of small and large intestine. Liver and gall bladder (*e*, *f*), pancreas (*g*), and spleen are present. A blind sac (the bursa Fabricii), the paired ureters (*m*), and the sexual ducts (*n*) open into the cloaca. The latter show the peculiarity that the right oviduct and ovary are degenerate, while those of the left side are correspondingly larger. Since copulation occurs the large eggs (the 'yolk') are fertilized in the oviduct (fig. 99). As they pass slowly through the duct, they become enveloped first with a thick layer of albumen, 'white' (*w*), then with a double egg membrane (*ism*, *sm*,) the two parts being separate and enclosing an air chamber at the larger end of the egg. Lastly comes the shell. All of these accessory structures are secreted by the glandular walls of the enlarged oviducts. During the passage down the oviduct the first phenomena of development (segmentation, gastrulation) occur, and after oviposition the development stops and again starts when the necessary warmth is supplied.

The care for the young, the sexual life connected with copulation, and the complicated conditions of existence connected with flight have resulted in an intelligence far superior to that of the reptiles, which finds its expression in the better development of sense organs and brain. In the brain (fig. 641) the cerebellum, which is the central organ for the coordination of the action of parts, is strikingly developed. Correspondingly large are the cerebral hemispheres, the frontal lobes of which begin to cover the olfactory lobes, the temporal lobes in like manner extending back over the 'twixt brain and optic lobes. Corresponding to the vocal apparatus, the ear is highly organized, the lagena of the labyrinth being greatly enlarged and the sound-conducting apparatus (columella, tympanum,

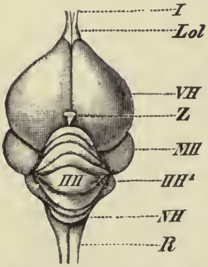


FIG. 641.—Brain of pigeon. (From Wiedersheim.) *HH*, vermis; *HH'*, hemispheres of cerebellum; *I*, olfactory nerves; *Lol*, olfactory lobes; *MH*, optic lobes; *NH*, medulla; *R*, spinal cord; *VH*, cerebrum; *Z*, pinealis.

etc.) well developed. The beginnings of an external ear are seen in the deeper position of the drum membrane. Since the power of flight necessitates vision at great distances, most birds have exceedingly sharp sight, and the eye itself (fig. 642) is in general constructed for distance. Peculiarities of the bird's eye, already weakly developed in the reptiles, are the pecten (*P*), a comb-shaped growth of the choroid into the vitreous body, and the scleral ring, a circle of bones developed in the sclera and supporting the outer part of the eye.

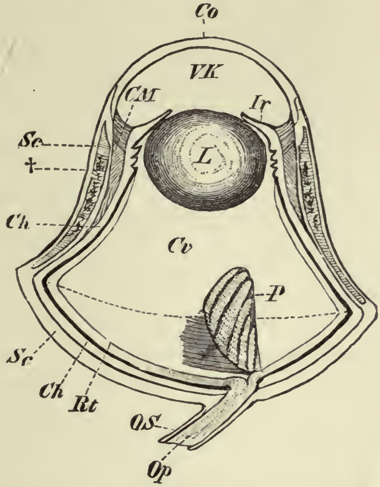


FIG. 642.—Eye of owl. (From Wiedersheim.) *Ch*, choroid; *CM*, ciliary muscle; *Co*, cornea; *Cv*, vitreous body; *Ir*, iris; *L*, lens; *Op*, optic nerve; *OS*, sheath of nerve; *P*, pecten; *Rt*, retina; *Sc*, sclera; *VK*, anterior chamber; †, sclerotic bones.

Among birds there is spirited rivalry for the females, especially among polygamous species. At the time of mating the males seek to win the favor of the females either through striking motions (dances), by singing, or by beauty of plumage. All of these peculiarities are confined to the male and frequently lead to a marked sexual dimorphism. The distinction in plumage is commonly strengthened at this time, the male receiving the brilliant wedding dress. Thus we speak of the spring molt, although there is only a color change and only exceptionally a renewal of the feathers. The return to every-day clothes only occurs with a molt, and this comes at the close of the reproductive season.

The reason for the dull plumage of the female is due to the fact that she usually sets on the nest, at which time inconspicuous colors protect her from destruction by enemies. In only a few instances is the heat necessary for incubation produced by other causes, such as the heat of the sun upon the sand in which the eggs are buried, or the increase of temperature caused by fermentation in decaying vegetation (Megapodes). The rule is that both sexes build the nest, which with the weaver birds is most skilfully constructed; occasionally among social species the nests are placed under a common roof. When the clutch of eggs is complete the female (rarely the male) begins the incubation, at this time in some instances losing the feathers from certain regions the better to warm the eggs. Many birds, like hens and ducks, are so far advanced when they leave the nest that they can follow the mother and feed themselves. Such birds are called Præcoces—in contrast to the Altrices, which hatch with incomplete coat of feathers and therefore need the warmth of the nest and the protection and care of the parents.

The migrations of birds possess great interest. We distinguish among birds permanent residents and others which, in order to obtain food, take long journeys, the migratory species. At the approach of cold weather these seek the south, following regular paths in their travels. They cannot, like reptiles and amphibians, hibernate at the period when insects and fruit are scarce, because their greater intelligence and their more energetic vital processes demand a more rapid metabolism and a continuous food supply. Hence the birds, like the mammals, in contrast to the 'cold-blooded' reptiles, amphibia, and fishes, maintain, under all extremes of external temperature, a body heat of 38–40° (44° ?) C. (100–104° F.).

The classification of birds is in a state of change. The older system based upon adaptive characters is not in harmony with the results of careful anatomical study, which would divide the whole class into many small groups. For this reason it has been thought best to retain the older system of larger, easily recognized divisions, and to call attention, where necessary, to the contradictions with later results.

Order I. Saururæ.

The view that birds are closely related to reptiles has received considerable support by the discovery of fossil birds with teeth. The most reptilian of these occur in the Jurassic of Bavaria, and only two specimens have been found. In these (*Archæopteryx lithographica*) the carpals and metacarpals have not fused, the three fingers are well developed and clawed, and the caudal vertebræ, although bearing feathers, form a long slender tail like that of a lizard (fig. 2).

Order II. Odontornithes.

These forms, from the cretaceous of Kansas and Colorado, also had teeth. In the ODONTORMÆ (*Ichthyornis*) there was a keeled sternum and normal pygostyle. In the ODONTOHOLCÆ (*Hesperornis*) the wings were reduced (only the humerus persisting), the sternum was without a keel, and the caudal vertebræ formed a broad paddle.

Order III. Ratitæ.

Here are included several families, very different in structure, which agree in having the feathers not arranged in feather tracts;

and in that, together with the lack of flight, many structures normally connected with it are absent. The bones are but slightly pneumatic, the sternum has no keel, and a furcula is not formed, the clavicles being rudimentary (*Dromæus*) or not present as distinct bones. The wings are small and lack primaries and secondaries adapted for flight, for typical contour feathers with close vanes, as well as typical down feathers, are absent.

Since several structures apparently adapted for flight occur here (fusion of hand bones and often of caudal vertebræ; arrangement of wing muscles), it is probable that the Ratites have descended from carinate forms by loss of power of flight. The anatomical distinctions between the various families lead one to believe that they have arisen from different groups of carinates and hence do not form a natural assemblage.

Section I. STRUTHIONES, with long humerus, long legs and neck. STRUTHIONIDÆ, two-toed ostriches of Africa, *Struthio camelus*. RHEIDÆ, South American three-toed ostriches, *Rhea americana*, nandu. Section II. CASUARINA; three toes, humerus short. *Dromæus*, emus; *Casuarius*, cassowaries. Section III. APTERYGES, bill long, nostrils near the tip, rudimentary wing skeleton; four toes. *Apteryx*, kiwi, of New Zealand. The DINORNITHIDÆ, three toes, wing skeleton absent; giant birds (thirteen feet high) of New Zealand; now extinct, but apparently contemporaneous with man. The *Æpiornis*, a gigantic bird of Madagascar, possibly belonged near these. Skeletons and eggs holding two gallons found in alluvium.

Order IV. Carinatæ.

The name refers to the presence of the keel to the sternum, which is correlated with the powers of flight possessed by most species. Other characters of the class are the presence of rectrices and remiges on tail and wings, and the fusion of clavicles to a furcula. There are strong fliers, like the raptores and albatrosses, which have but a small carina; in many poor fliers the carina may be entirely absent. The furcula is not always present, the clavicles not uniting (many parrots and toucans) or being absent (*Mesites*). The remiges are also degenerate in some carinates, as in the penguins (which are flightless, although they have a strong carina), where they take the shape of small scales. Thus the distinctions between ratite and carinate birds vanish in places.

Sub Order I. GALLINACEA. The hen-like birds are praecoces with compact bodies and well-developed wings and legs, so that they run and fly well without excelling in either direction. The feet have three toes in front, usually connected by a membrane at the base (fig. 643, *c*); the fourth toe is behind and at a higher level. Above this in the male is usually the spur, a process of the tarso-metatarsus, covered with horn. The margins of the upper jaw overlap the lower; the beak is bent downward at the tip and is about as long as the head. Naked, richly vascular lobes form comb and wattles which are specially large in the more elegantly plumaged males.

The PHASIANIDÆ are polygamous; *Phasianus*, with many species of pheasants; *Gallus bankiva* of the Sunda Islands, the ancestors of domestic fowl. *Meleagris,** the turkeys. The TETRAONIDÆ are partly polygamous, partly monogamous. *Coturnix,** quail; *Perdix,** partridge; *Bonasa,** grouse. The incubation of the Megapodes has been referred to (p. 611).

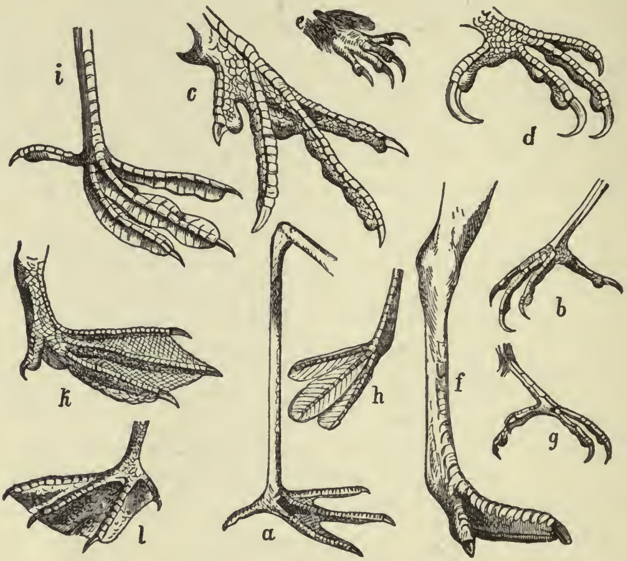


FIG. 643.—Foot forms. (From Schmarda.) *a*, semi-palmate, wading of *Ciconia*; *b*, perching of *Turdus*; *c*, rasorial of *Phasianus*; *d*, raptorial of *Falco*; *e*, adherent of *Cypselus*; *f*, cursorial of *Struthio*; *g*, zygodactyl (scansorial) of *Picus*; *h*, lobate of *Podiceps*; *i*, lobate and scalloped of *Fulica*; *k*, palmate of *Anas*; *l*, totipalmate of *Phaethon.*

Sub Order II. COLUMBINÆ. The pigeons are distinguished from the Gallinaceæ by the more slender bodies, shorter legs, the toes free, and the longer wings capable of prolonged flight. They are altrical; the crop produces a milky secretion used in feeding the young. The COLUMBIDÆ are the most widely distributed and are represented in the tropics by numerous beautifully colored species. *Columba.** According to Darwin the domestic pigeons come from *C. livia*, the blue rock pigeon; *Ectopistes migratorius*,* passenger pigeon, practically exterminated. Allied was the dodo, *Didus ineptus*, of Madagascar, exterminated in the eighteenth century.

Sub Order III. NATATORES. A number of families, while differing much in structure, are united by their inclination for an aquatic life. They are called swimming birds (Natatores) because, thanks to their webbed feet, they are excellent swimmers and divers. Either all four toes are connected by the web (totipalmate, fig. 643, *l*), or only the three anterior toes are webbed (palmate, fig. 643, *k*), or the three toes are each bordered with a swimming membrane (lobate, fig. 643, *h*). Thus the foot structure gives distinctions which forbid a closer association of the families, and this is strengthened by differences of wing and beak. On the other hand palatal structures show that here, as in the Grallatores, very diverse forms are associated.

Section I. LAMELLIROSTRES (Anseriformes), feet palmate; the beak soft-skinned up to the hard tip, its margins with transverse horny plates. *Anas boschas*,* wild duck, source of domestic breeds. *A. mollissima*, eider; *Anser*,* goose (domestic derived from *A. ferus*). *Cygnus*,* swans. Section II. TUBINARES (Longipennes), predaceous birds with strong beak, tubular nostrils, palmate feet, and long wings capable of rapid and prolonged flight. *Diomedea*, albatross; *Larus*,* gulls; *Sterna*,* terns. Section III. URINATORES. Birds with small wings, sometimes reduced to flippers, and upright position owing to position of the legs far back. The ALCIDÆ (*Alca impennis*,* the great auk, exterminated in the nineteenth century), which are northern and are related to the gulls, and the antarctic IMPENNES (*Aptenodytes* — fig. 644, penguin) agree in having palmate feet, but otherwise differ greatly in structure. Some of the COLYMBIDÆ (*Urinator*,* loons) have palmate feet, others (*Colymbus*,* grebes) have lobate feet. Section IV. STEGANOPODES, with totipalmate feet. *Pelecanus*,* pelicans; *Phalarocorax*,* cormorants; *Phaethon*,* tropic birds.

Sub Order IV. GRALLATORES. The wading birds affect swampy lands and the shores of the sea, ponds and streams, their legs being lengthened, chiefly by elongation of the tarso-metatarsus, the feet semipalmate (fig. 643, *a*), and the feathers only on the upper parts, the lower with horny plates, all features adapted to the wading life. Correlated is the striking length of neck and beak. These features have appeared in groups which are very different in anatomical characters.

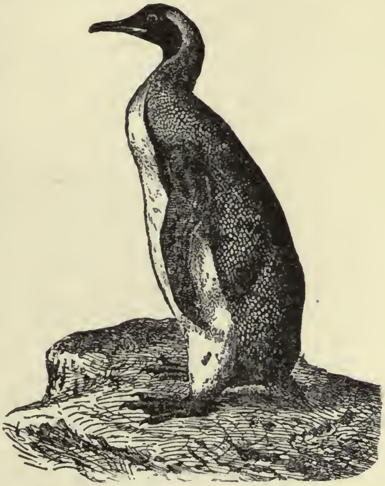


FIG. 644.—*Aptenodytes patagonica*, penguin. (From Brehm.)

Section I. CICONIFORMES. Beak with a strong horny coat. *Ardea*,* herons; *Ibis; Ciconia*, storks; *Phœnicopterus*,* flamingo. Section II. GRUIFORMES. Beak always with soft skin at the base, often extending to the tip. *Grus*,* cranes; *Rallus*,* rails; *Otis*, bustards, terrestrial. Section III. CHARADRIFORMES. Allied to the auks and gulls. *Scolopax*,* woodcock; *Charadrius*,* plover.

Sub Order V. SCANSORES. The climbing birds are readily recognized by their zygodactyle feet (fig. 643, *g*), in which two toes (*2* and *3*) are directed forwards, the other two (*1* and *4*) backwards. The forms united under this head differ much in structure and their association does not rest on blood-relationship.

Section I. CUCULIFORMES. The PSITTACI, or parrots, are brightly colored mostly tropical birds with short, high, compressed, and strongly bent beak and fleshy tongue. But one species (*Conurus carolinensis* *) in the United States. *Cacatua*, *Plictolophus*, cockatoos; *Melopsittacus*, *Psittacus*, parrots. CUCULI, bill slightly arched or straight; outer toe usually versatile; *Cuculus*, *Coccygus*,* cuckoos. Section II. PICARIÆ. The woodpeckers have a long, straight, conical beak and long, protrusible tongue; *Picus*.* Nearly allied are the toucans (*Rhamphastos*) of the tropics.

Sub Order VI. PASSERES. This is by far the richest in species of all the groups of birds. They are altrices of moderate size, with slender feathered tarsi and strong, horny beak without cere. Of the three anterior toes the two outer are either united or separated to the base (fig. 643, *b*), while the hind toe is at a level with the rest. In some, which are usually but not invariably noticeable for the powers of song of the males, there are special muscles to the syrinx which are lacking in other birds. These are called Oscines, in contrast to the other Passeres, the crying birds, or Clamatores. These groups are further distinguished by a large, freely movable hind toe in the Oscines, while in the Clamatores it is restricted in its motions.

Section I. OSCINES. All our song birds belong here: FRINGILLIDÆ, finches; *Passer domesticus*,* English sparrow; *Loxia*,* crossbills; ICTERIDÆ; *Icterus*,* orioles; *Dolichonyx*,* bobolink; ALAUDIDÆ, *Alauda*,* skylark; SYLVICOLIDÆ, *Dendrœca*,* *Helminthophaga*,* warblers; TURDIDÆ, *Turdus*,* thrushes; *Siala*,* bluebirds; HIRUNDINIDÆ, *Hirundo*,* swallows; TROGLODYTIDÆ, wrens; CORVIDÆ, *Corvus*,* crows; *Cyanocitta*,* jays. The PARADISEIDÆ, or birds of paradise, with marked sexual dimorphism, are closely related to the crows (fig. 15). Section II. CLAMATORES. Here are frequently included a few groups (COTINGIDÆ, TYRANNIDÆ) best developed in South America and the lyre birds (MENURIDÆ) of Australia. Earlier other forms were regarded as allied, but now are separated as Cypselomorphæ, or Coraciformes, and united with the owls and Picariæ. CYPSELEDÆ; *Chætura*,* chimney 'swallow,' with adherent feet (fig. 643, *c*). TROCHILIDÆ, humming birds, best developed in tropical America; *Trochilus*.* CAPRIMULGIDÆ, night hawks; *Antrostomus vociferus*,* whippoorwill. ALCEDINIDÆ, kingfishers, *Ceryle*.* BUCERONTIDÆ, horn bills, tropical.

Sub Order VII. RAPTORES. The birds of prey are strong birds of considerable size. They have the tarso-metatarsus feathered and four strongly clawed toes of what is termed the raptatorial type (fig. 643, *d*). The beak is strong, the upper half, strongly hooked at the tip, extending over the lower. There are two groups recognized which probably are not closely related.

Section I. FALCONIFORMES. Slender birds with close plumage and extraordinary sight; related structurally to the herons. CATHARTIDÆ, buzzards; *Cathartes aura*,* turkey buzzard. Pandionidæ, *Pandion haliætus*,* fish hawk; Falconidæ: *Aquila*,* *Haliætus*,* eagles; *Buteo*,* buzzards; *Falco*,* falcons; *Accipiter*,* hawks. Section II. STRIGES, owls; compact birds with loose, fluffy plumage, large eyes in a circle of feathers; more closely related structurally to the Caprimulgidæ than to the Falconiformes. *Bubo*,* horned owls; *Scops*,* screech owls; *Strix*,* gray and brown owls; *Speotyto*,* burrowing owls.

Class III. Mammalia.

The mammals occupy the highest place among the vertebrates, and consequently in the animal kingdom; they also possess a special interest for us, for man, in structure and development, belongs to the group, although separated in intelligence from the most highly organized of the members by a wide gap.

The most striking characteristics of the mammals again are furnished by the skin. In fact one may, with Oken, call them hair-animals, since hair is as diagnostic as feathers are for birds. The hairs (fig. 645, *H*) are cuticular structures which are seated on papillæ of the derma, and are nourished by blood-vessels in these. The lower end, the root of the hair, lies in a pit in the epidermis, the hair follicle, and is surrounded by a double envelope, the epithelial root sheath, formed by an inpushing of the epidermis and an outer connective-tissue follicular sheath. Small muscles attached to the base of the larger hairs serve for their erection.

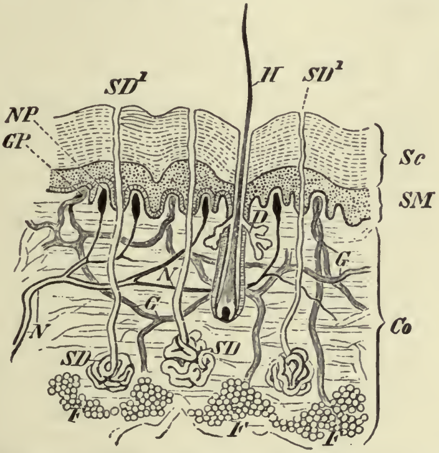


Fig. 645.—Section of skin of man. (From Wiedersheim.) *Co*, derma (corium); *D*, oil gland; *F*, fat; *G*, blood-vessels; *GP*, vascular papilla; *H*, hair; *N*, nerves; *NP*, nerve papilla; *Sc*, stratum corneum; *SD*, *SD'*, sweat gland and duct; *SM*, stratum Malpighii.

Since side branches are lacking, the structure of the hair is more simple than that of feathers, and the forms fewer. Wool is characterized by its spiral turns; then there is straight hair which, by increase in size, forms the 'whiskers' (vibrissæ) on the upper lip of many mammals, bristles (swine), and lastly the spines of hedgehogs and porcupines. In the pelts of many animals two kinds of hair may occur, wool below and straight hair outside. Histologically hair consists of cornified cells, often arranged in medullary and cortical layers. On the outside there may be another layer recalling the pseudocuticula of reptiles. In most mammals there is a periodic shedding and renewal of the hair, the new hair arising from the old follicle (? from the old papilla). Ordinarily this occurs only in spring. Besides hair some mammals have true scales. Constant horny structures are the armatures of the tips of the digits, which, according to form, are divided into claws (ungues), hoofs (ungulæ), and nails (lamnæ).

The old view that the hair, like feathers, corresponds to the scales of reptiles has recently found both defenders and opponents, the latter thinking it probable that the hair has arisen from the nerve-end structures of aquatic vertebrates. The claws, together with those of reptiles and birds, must have come from horny scales, which indeed occur in many amphibia as hollow cones capping the toes. The dorsal part of this scale, the claw plate, becomes especially strong, its formation taking place at the base, the root, from whence it is forced forward over the bed (in man the limit of nail formation is shown by the lunule). The ventral part of the scale, the subungua or solenhorn, is poorly developed in true claws because its region is restricted by the arching of the claw plate in both directions, but is more evident in hoofs, in which the plate is curved only horizontally. In the horse it forms the 'sole,' lying between the frog and the hoof. It is rudimentary or entirely lost in the nails of apes and man.

The skin of mammals is further characterized by its richness in glands, of which, with few exceptions, there are two kinds, sebaceous and sweat glands. The first are acinose glands, and usually open in the hair follicles, giving the hair the required oiliness (fig. 645, *D*). The sweat glands, except in the monotremes, are entirely independent of the hairs, and are simple tubes, coiled at their deeper ends (*SD*), secreting a fluid sweat which is of great value in the preservation of a constant temperature, its evaporation cooling the body. Under the influence of sexuality the glands in certain regions, and especially the sebaceous glands, develop great activity and form considerable glandular pouches or pockets: caudal and anal glands of many carnivores, hoof glands and suborbital glands of ruminants, musk and castor glands of musk deer and beaver (fig. 652, *a*). More important than these are the modifications of dermal glands into mammary or milk glands, which, indeed are so characteristic that they have given rise to the name mammalia. These are almost invariably sebaceous glands (in the monotremes sweat glands) which empty in great numbers upon a restricted area of the skin, which, except in monotremes, is elevated into true nipple (fig. 646, *A*), or around which the adjacent skin becomes elevated in tubular form (*B*) as in the cows. The mammæ are always symmetrically arranged upon the ventral surface, sometimes in the breast region, but more frequently in the inguinal region. There are at least two, usually more (22 in *Centetes*). In general the number corresponds to the maximal number of young at a birth.

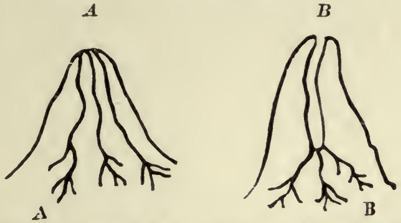


Fig. 646.—*A*, true, *B*, false nipple. (After Gegenbaur.)

A dermal skeleton occurs in few species (*e.g.*, the firm bony plates of the armadillos); on the other hand the axial skeleton shows many features not occurring elsewhere. In the skull many of the bones already referred to are evident only as centres of ossification, fusing early with their neighbors to form larger bones. As the temporal bone shows, parts of diverse origin may fuse—parts of the visceral skeleton and parts of the cranium; membrane and cartilage bones—so that a sharp line between cranial and facial portions cannot be drawn. So it becomes necessary in describing the skull not to follow exactly the model adopted so far, but to take that of human anatomy.

In the hinder region of the skull is a large occipital bone (figs. 561, 562), jointed to the atlas by double occipital condyles, and arising by the fusion of the four bones of the occipital region. Besides it includes usually a membrane bone, the interparietal, which occurs only in mammals. This is, strictly speaking, a paired bone, arising in the angle between the parietal and the supraoccipital and fusing with the latter. In front of it lie in the roof of the cranium, as in other vertebrates, the parietals (fused with the interparietals in many ruminants and rodents), the frontals and nasals, the lachrymals being always associated with them. In the floor of the cranium the sphenoid bone lies in front of the basioccipital portion of the occipital. In many mammals this consists of an anterior and a posterior portion throughout life; in man this condition occurs at least in the embryo. Each of these parts in development consists of three elements, the posterior of the basisphenoid as the body, and the paired alisphenoids (great wings); the anterior is similarly composed of the presphenoid and the paired orbitosphenoids (lesser wings) (fig. 562, *Spb*, *Ps*, *Als*, *Ors*). In front of the sphenoid lies the ethmoid, *Eth*, likewise formed from three parts, the mesethmoid, which forms a partition between the two nasal cavities, and the paired ectethmoids, which form the lateral walls of the nasal cavities. These last have complicated folds on their inner surface, the superior and middle turbinated bones, which support the olfactory membrane, thus greatly increasing its surface. With these is associated the os turbinale, a distinct bone, the inferior turbinated bone of human anatomy.

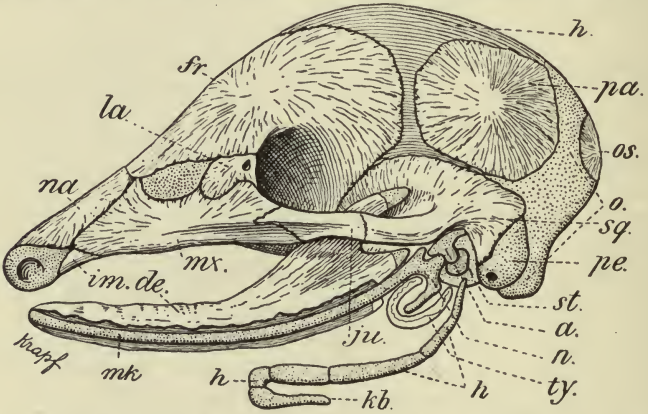


Fig. 647.—Skull of embryo *Tatusia*. (After Parker, from Wiedersheim.) Cartilage dotted, membrane and membrane bones lined. *a*, incus (quadrate); *de*, dentary; *fr*, frontal; *h*, (above) membrane over anterior fontanelle, (below) hyoid bones; *im*, premaxillary; *ju*, jugal (malar); *kb*, remnants of gill arch; *la*, lachrymal; *mk*, Meckel's cartilage; *mx*, maxillary; *n*, malleus (articulare); *na*, nasal; *o*, occipital cartilage; *os*, supraoccipital; *pa*, parietal; *pe*, petrosal; *sq*, squamosal; *st*, stapes; *ty*, tympanic.

The temporal bone, which is intercalated between the roof and floor of the skull, can only be understood by its embryonic relations and its connexion with the first and second visceral arches (fig. 647). Its centre is formed by the petrosal (*pe*), developed in the walls of the otic capsule, to which, as elsewhere in the vertebrates, are attached: (1) the cartilaginous jaw arches, the quadrate (*a*), and the mandibular (*n* and *mk*); (2) the cartilaginous hyoid arch, the stapes (in part equalling the hyomandibular, *st*), and the hyoid proper (*h*) (compare with the visceral skeleton of the selachian, fig. 588). To these are added the membrane bones, the squamosal (*sq*), at the base of the quadrate, which increases as the latter loses in size, and below the squamosal the tympanic (*ty*). With ossification of the cartilaginous parts several centres form the petrosum, which fuses with the squamosal, and frequently with the tympanic, which in some forms enlarges to a conspicuous bulla ossea. Petrosum and squamosal on the one side, tympanic on the other, enclose a space, the tympanic cavity, into which the upper parts of both visceral arches extend, ossifying into the ear bones, the quadrate to the incus, the hyomandibular possibly to stapes (fig. 577).

The tympanic in uniting with the squamosal (forming Glaser's fissure) encroaches on the mandibular cartilage so that the upper end (*n*), which is homologous with the articulare of other vertebrates, is enclosed in the tympanic cavity and, along with a second bone, the angulare, ossifies to form the malleus, while the lower portion, Meckel's cartilage proper (*mk*), becomes pinched off. Meckel's cartilage gradually disappears; on the other hand the surrounding membrane bone, the dentary (*de*) increases and alone forms the lower jaw, which now forms a new articulation with the squamosal. It will be noticed that the old articulation was between cartilage bones, the new between membrane bones developing around the cartilages. (There is, however, some evidence to show that the mammalian lower jaw consists of several bones, some of them preformed in cartilage, and that one of these forms the articulation with the squamosal.)

The lower part of the hyoid arch, the hyoid, remains outside the ear and often fuses with the petrosal. The upper end (styloid process) may then become entirely separate from the lower, which becomes attached to the copula (body of hyoid) as the anterior horn, the connecting cartilage being reduced to a stylohyoid ligament. In the hyoid of mammals there is also included a remnant of a gill arch as the posterior horn.

As the quadrate, by its modification into the incus, becomes strikingly reduced, the rest of the arch—vomer, palatine, and pterygoid—is poorly developed in contrast to the large maxillary bones. Premaxillaries and maxillaries (fused in man to a single bone) form an important element in the face, and send backwards and inwards palatine processes into the roof of the mouth. These encroach upon the bones of the palatal series; the vomers of the two sides are pressed together to a single bone lying vertically entirely within the nasal partition; the palatine and pterygoid are forced backwards. The palatines contribute to the hard palate, the pterygoids only exceptionally (Cetacea, many edentates); the latter usually lose their independence and fuse with the nearest bone of the base of the cranium, the basisphenoid (more accurately with a process of the basisphenoid, the lamina externa of the pterygoid process, the pterygoid forming the lamina interna). Thus the hinder sphenoid, like the temporal, contains cranial and visceral elements.

In the vertebral column the cervical and the rib-bearing thoracic vertebræ are always distinct, and the same, with the exception of the Cetacea and Sirenia, is true of lumbar, sacral, and caudal vertebræ. Of sacrals there is one in all embryos, and throughout life in the marsupials, elsewhere from two to five, rarely, as in edentates, as many as thirteen. The number of vertebræ in each group is rather restricted. Thus, except in *Bradypus tridactylus* (9), *Cholœpus hoffmanni* and *Manatus* (6), the number of cervicals is always seven.

Of the appendicular skeleton the girdles are most interesting. The coracoid, which in monotremes reaches the sternum, is reduced in all other mammals to a small coracoid process of the scapula. More rarely the clavicle is lacking (rapid runners); in the monotremes it extends to the episternum (fig. 648, *Cl*, *Ep*); elsewhere it appears to articulate with the sternum, in reality by the intervention of interarticular cartilages (once regarded as a rudimentary episternum, now called preclaviæ). In the pelvis all three elements are fused to a single os innominatum; pubis and ischium unite ventrally with each other, enclosing between them the obturator foramen (fig. 655). The pubes of the two sides unite by a symphysis which can extend back to the ischia.

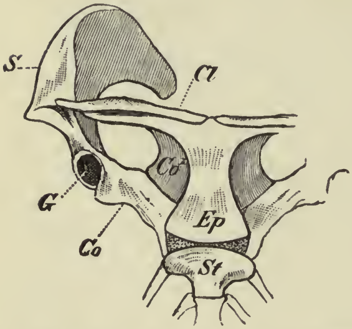


Fig. 648.—Sternum and shoulder girdle of *Ornithorhynchus paradoxus*. (From Wiedersheim.) *Cl*, clavicle; *Co*, *Co′*, coracoid; *Ep*, episternum; *G*, glenoid fossa for humerus; *S*, scapula; *St*, manubrium sterni (anterior element of sternum).

Since the mammals in general are distinguished from other vertebrates by their intelligence, the brain is characterized by the size of cerebrum and cerebellum (fig. 649). In contrast to birds and fishes, the cerebellum (*IV*) is differentiated into a median vermis and lateral cerebellar hemispheres. In the cerebrum the mantle comes first into consideration. Its frontal lobes grow forwards over the olfactory lobes, which consequently lie farther and farther back on the lower surface. The temporal lobes extend right and left over the optic lobes and down to the floor of the cranium; the occipital lobes cover successively the mid brain, cerebellum, and medulla oblongata. Since the greatest increase of intelligence lies within the mammals, the cerebra may be arranged in an ascending series. In the monotremes, marsupials, insectivora, and rodents (fig. 649, *A*) the olfactory lobes are visible in front, usually the mid brain behind (*III*). In the lemurs, carnivores (fig. 649, *B*), and ungulates the olfactory lobes are completely, the cerebellum partly, covered. In man and the anthropoid apes, on removing the roof of the skull, only the two cerebral hemispheres are visible, all other parts being more or less completely covered.

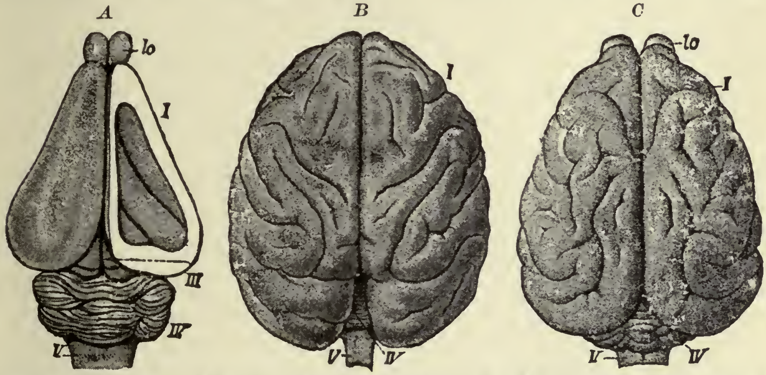


FIG. 649.—*A*, brain of rabbit (after Gegenbaur); *B*, of fish otter. *C*, of pavian monkey (after Leuret and Gratiolet). *I*, cerebrum; *III*, optic lobes; *IV*, cerebellum; *V*, medulla oblongata; *lo*, olfactory lobes.

Further, it is to be noted that in the first group the surface of the cerebrum is smooth, while in the others the cortex is increased by infolding and the formation of convolutions (gyri and sulci) which reach their greatest complication in the anthropoid apes and especially in man. A consequence of the increase in size of the brain is the great development of the connecting nerve tracts, which become more and more prominent as parts of the brain. Thus the two halves of the cerebrum are connected by a large transverse tract, the corpus callosum; two solid cords, the crura cerebri, run back from the cerebrum to the other parts, while a transverse commissure, the pons Varolii, passes below, connecting the two sides of the cerebellum. These connexions in the other vertebrates are small, and even in the lower mammals, like monotremes and marsupials, are but slightly developed.

The increase of cerebrum and cerebellum, which occurs chiefly in the dorsal portion, has resulted in flexures in the axis of the brain, already indicated in the reptiles, increased in the birds, and reaching their maximum in the mammals. Instead of continuing in the course of the spinal cord, the axis of the brain bends ventrally in the medullar region (cervical flexure), then in the region of the pons again dorsally (pontal flexure), an at the level of the optic lobes again ventrally (cephalic flexure). By its increase in size the brain has influenced the skull in an interesting way; for, while even in birds the brain is almost entirely confined to the region behind the eyes, in the higher mammals it has extended forward to the olfactory region. Thus there comes an increase of the cranium at the expense of the face. The relative sizes of the two were adopted by Camper as an index of intelligence, and were measured by 'Camper's angle,' a method which has since undergone considerable improvements.

Of the sense organs the nose is characterized by three features. An outer nose, supported by cartilage and often extended as a proboscis, has been formed. Its cavity has been increased, since by the formation of hard and soft palate a part of the primitive mouth cavity has been included in it. Its upper portion, the olfactory region, has been complicated by the formation of olfactory folds, supported by the turbinated bones already referred to (p. 620). To increase the mucous surface there are extensions of the nasal cavity, frontal, maxillary, and sphenoidal sinuses, into the corresponding bones. The eye has the upper and lower lids, besides the nictitating membrane in a more or less reduced condition. The ear, except in monotremes, Cetacea, Sirenia, and some seals, has a conch supported by cartilage, while the external auditory meatus is always present. Internally the ear is much modified, since the three bones, malleus, incus, and stapes (p. 544), occur nowhere else, while the lagena has been greatly lengthened, coiled into a spiral with two to four turns (figs. 80, 576), while inside the wonderful organ of Corti has been developed.

Of digestive structures, the teeth—which are restricted to maxillary, premaxillary, and dentary bones—need special mention, because of the distinctions they afford from all other vertebrates, and because of their importance in differentiating the various orders. If we omit the monotremes, edentates, and whales, in which there is marked degeneration in the dentition, there are four particulars which show the dentition of mammals more developed than that of other vertebrates. (1) The number of teeth is constant for the species, usually for the genus, and often for the family. As man normally has thirty-two teeth, so the dog has forty-two, the anthropoid apes thirty-two, the platyrhine apes thirty-six, etc. (2) The teeth are firmer. The body of dentine is divided, by a slight constriction, into a crown covered with enamel, and a root enveloped in cement (bony tissue). The roots are placed in separate sockets (alveoli) in the jaws, and in those cases where continuous growth is necessary the pulp persists and the teeth, as in the incisors of rodents and the tusks of elephants and pigs, grow indefinitely. (3) In consequence of their greater firmness the teeth are not used up so fast and do not require rapid replacement. There occurs only one change, in which the dentition present at birth or developed soon after—the milk, or lacteal, dentition or, better, first dentition—is replaced by the second or permanent dentition (diphyodont mammals). In some cases (monophyodont mammals) there is no change, the first dentition being permanently retained (marsupials, perhaps toothed whales), or the first dentition is more or less rudimentary (edentates, many rodents, bats, seals, some insectivores). Besides the two typical dentitions traces of a third or even of a fourth may occur. A prelacteal dentition of calcified germs which are never functional is best seen in marsupials, and is rare in placental mammals. A dentition following the permanent one is outlined in many placentalia, and some of its teeth may exceptionally come into function. (4) Among the teeth a division of labor has brought about change of form (heterodont dentition). The teeth of the premaxillaries and their antagonists in the lower jaw are single-rooted and usually have more or less a chisel shape, hence they are called incisors even when, as in insectivores, the crowns are needle-like (fig. 661). Behind the incisors (in the maxillary bone in the upper jaw) is the canine tooth (fig. 650, *c*), which is single-rooted and has usually a conical crown (probably a modified premolar). Following the canine come the molars, broad teeth mostly with two roots and tubercular crowns. Only the anterior ones appear in the milk dentition, while the others appear only in the permanent dentition and are not replaced. On this develop-

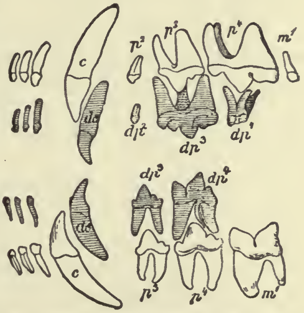


FIG. 650.—Permanent and milk dentitions of the cat. (From Boas.) c, canines; p^2–p^4, premolars; m', molar (the milk dentition darker and each letter preceded by *d*).

mental basis the molars are divided into premolars (bicuspids of dentists), which appear in both dentitions, and the true molars, which occur only in the last.

From the foregoing it will be seen that every species of mammal is characterized by its dentition, and these features may be expressed by a short formula. It is only necessary to place the number of each of the four kinds of teeth mentioned in their regular order, those of the upper jaw separated from those of the lower by a horizontal line, to express this. Since the two sides of the body are symmetrical, only those of one side need be enumerated, and in case that one kind be absent the deficiency is indicated by a zero. The dental formula of man would thus be $\frac{2\,1\,2\,3}{2\,1\,2\,3}$; of the reindeer, in which in the upper jaw incisors and canines are absent, $\frac{0\,0\,3\,3}{3\,1\,3\,3}$. The different formulæ, by comparison, give us a fundamental formula from which they have been derived by reduction. This was probably $\frac{4\,1\,4\,4}{4\,1\,4\,4}$.

The molars undergo, according to the food, the greatest modification of form. As a starting point the bunodont tooth may be taken which occurs in omnivorous mammals and which has the crown with several blunt projections or cones. With animal food (fig. 650, 657) the cones become sharper and cutting (secodont dentition of carnivores and insectivores), and when the cutting angle becomes very sharp, with a special prominence on the inner side, it is spoken of as a flesh or carnasial tooth. In vegetable feeders the cones become connected by crests (lophs) or are half-moon-shaped (lophodont or selenodont). Since the cones and lophs become in part worn away and the grooves between them are filled with cement, there arise broad grinding surfaces strengthened by the harder and more resistant enamel of the cones and lophs; this extends inwards as folds from the outer enamel wall of the tooth; the folds may become cut off and form islands of enamel on the grinding surface (dentes complicati of ungulates). When the folds extend in regular order from the outside and inside and meet in the middle they form numerous successive leaves, bound together by cement (compound teeth of elephants, fig. 667, and many rodents).

Paleontological investigation, with which the more recent embryological results are in accord, has shown that a great regularity prevails in the formation of the cones of the molars. Triconodont and tritubercular teeth are recognized, in which the three cones are either arranged in a line or in a triangle, as well as multitubercular teeth with more numerous cones irregularly arranged. The triconodont type develops farther by the formation of secondary cones. The development of these occurs in different ways in molars and premolars. Since the latter are the more simple, their distinction from the molars does not rest alone upon the existence of a milk dentition, but upon structure as well. This is important, because it happens that there are premolars which are not replaced (marsupials, many insectivores and rodents) and, on the other hand, beneath the molars the anlagen of replacing teeth may be found. The latter fact shows that the molars, strictly speaking, belong not to the permanent but to the milk dentition. They are late in formation and are therefore parts of the first dentition carried over into the second.

The mouth, which contains tongue and teeth, is separated from the next division of the alimentary tract, the pharynx, by the uvula. The pharynx narrows behind into the œsophagus, the entrance of which into the stomach is marked by a constricting cardia. At its other end the stomach has a similar constrictor, the pylorus, separating it from the intestine. In the latter small and large intestines (the latter consisting of colon and rectum) are differentiated by the diameter of the lumen. The small intestine opens laterally into the colon and at the junction arises a blind diverticulum, the cæcum, which is small in mammals with animal food, but in herbivores (especially rodents) is always large and forms a conspicuous part of the alimentary tract. The vermiform appendix (primates, rodents) is a narrower part of the cæcum. Three pairs of salivary glands empty into the mouth, the liver and pancreas into the small intestine (duodenum).

Most important of respiratory peculiarities is the diaphragm, which separates the body cavity into thoracic and abdominal cavities. This occurs only in its beginnings in other vertebrates (perhaps even in Amphibia). In the thoracic cavity are the œsophagus, heart with its pericardium, and especially the trachea, bronchi, and lungs; the remaining vegetative organs are in the abdominal cavity. The diaphragm is a muscular dome, its convex side towards the thoracic cavity; by contraction it flattens an increases the size of the cavity, in consequence of which air is drawn into the lungs (inspiration). On relaxation the lungs contract from their own elasticity and force out a part of the air (expiration). The intercostal muscles, which raise and lower the framework of the chest, also play a part, as in birds. The respiratory ducts (fig. 579) begin with the larynx (with vocal cords), which can be closed from the pharynx by the epiglottis; this is followed by the trachea, which divides into right and left bronchi. Each bronchus divides again and again, and the finest of these divisions, the bronchioles, are continued as alveolar ducts to small chambers, the infundibula, both these and the alveolar ducts being lined with small respiratory pockets, the alveoli.

The heart, with two auricles and two ventricles, is completely separated into systemic and pulmonary halves. In early embryonic life the arterial trunk, which at first is simple, is divided into a pulmonary artery, arising from the right half of the heart and carrying venous blood, and an aorta ascendens, with arterial blood, connected with the left half. In contrast with the reptiles, the right aortic arch is entirely lost, the left persisting.

The urogenital system is of great importance in the separation of the group into smaller divisions (fig. 651). In both sexes this consists of practically the same parts in early embryonic life. These are the early formed Wolffian body (*W*); the permanent kidneys, which appear later and are not shown in the diagram; the urinary bladder (*4*), a part of the allantois which extends (*5*) into the fœtal appendages; the three ducts, the Müllerian (*m*), the Wolffian (*w*), and the ureter (*3*). These ducts no longer empty into the intestine, but into the allantoic structures, the ureters into the base of the urinary bladder, the Wolffian and

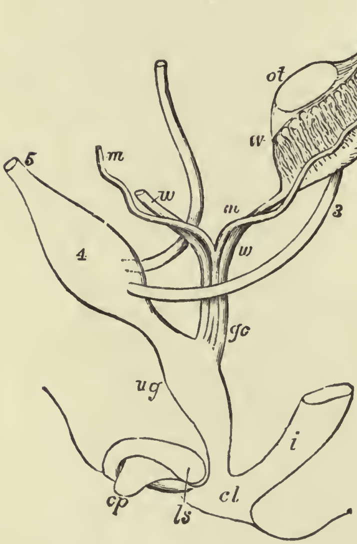


FIG. 651.

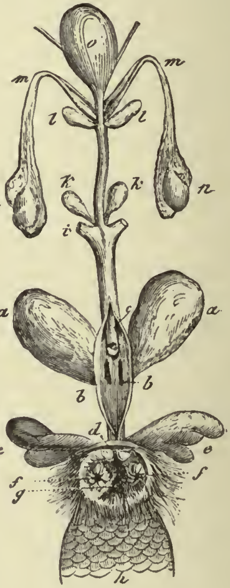


FIG. 652.

FIG. 651.—Diagram of embryonic mammalian urogenital system. (From Balfour, after Thompson.) *cl*, cloaca; *cp*, genital process; *go*, genital cord; *i*, rectum; *ls*, ridge for formation of labia or scrotum; *m*, Müllerian duct; *ot*, gonad; *ug*, urogenital sinus; *W*, Wolffian body; *w*, Wolffian duct; *3*, ureter; *4*, urinary bladder; *5*, continuation of latter to allantois (urachus).

FIG. 652.—Urogenital system of male beaver. (From Blanchard.) *a*, castoreum sacs; *b*, openings of their ducts into preputial canal; *c*, tip of penis; *d*, preputial opening; *e*, anal glands; *f*, their ducts; *g*, anus; *h*, base of tail; *i*, corpora cavernosa; *k*, Cowper's glands; *l*, seminal vesicles; *m*, vasa deferentia; *n*, testes; *o*, urinary bladder with ureters.

Müllerian ducts into the urogenital sinus (*ug*), the lower continuation of the bladder. The gonad is connected with the Wolffian duct. In the anterior wall of the urogenital sinus is a mass of highly vascular tissue (*cp*), from which and a surrounding fold the external genitalia are developed. Since the urogenital sinus opens from in front into the intestine, there is always a claoca (*cl*) in the embryonic stages, which persists throughout life in the monotremes, and to a considerable extent in the female marsupials; in all other vertebrates it is divided by a partition, the perinæum, into a urogenital opening in front and an anal opening behind.

From this indifferent condition the male and female apparatus are derived, the structures being closely similar in most males (fig. 652). The Müllerian duct vanishes, while the Wolffian duct becomes the vas deferens and its accessories, serving as a canal for the genital products, while the external genitals arise from the other parts mentioned, these forming an intromittent organ (penis). In the female the Wolffian body and duct degenerate, the Müllerian ducts become the reproductive canals. The modifications of these become of great systematic importance. In the monotremes both ducts open separately and become differentiated into two parts (fig. 653, *A*), anterior oviducts with wide openings into the body cavity (*od*, *t*) and the uterus (*u*). The ureters open into the sinus (and not into the bladder) between the uterine openings. In the marsupials (*B* and *C*) there are three divisions, oviduct, uterus, and vagina; besides, the two Müllerian ducts may approach, near the uterus (*B*), or fuse in this region (*C*) in some

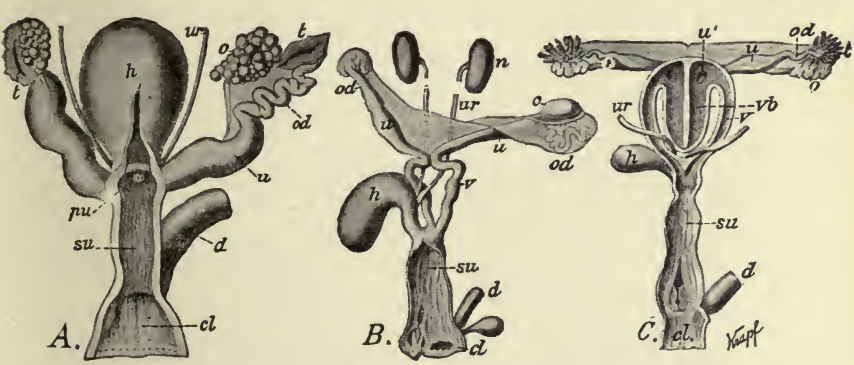


FIG. 653.—Female genitalia of (*A*) *Echidna aculeata;* (*B*) of *Didelphys dorsigera;* (*C*) *Phascolomys wombat.* (*B* and *C*, after Wiedersheim.) *cl*, cloaca; *d*, rectum; *h*, urinary bladder; *n*, kidney; *o*, ovary; *od*, oviduct; *pu*, month of ureters; *su*, urogenital sinus; *t*, ostium abdominale tubæ; *u*, uterus; *u'*, opening into vagina; *ur*, ureter; *v*, vagina; *vb*, vaginal blind sac.

species, forming an unpaired blind sac (*vb*), which may even open into the urogenital sinus as a third vagina. This partial fusion of the vaginæ of the marsupials is completed in the placental mammals, the single vagina and the sinus forming a single canal (fig. 654). Here the uterine portions may remain distinct (uterus duplex of rodents, *A*), or they may fuse partially (uterus bicornis of insectivores, whales, ungulates, and carnivores, *B*), or they may be completely fused (uterus simplex of apes and man, *C*).

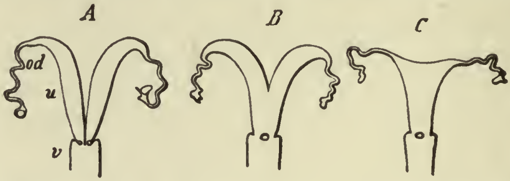


Fig. 654.—*A*, uterus duplex; *B*, uterus bicornis; *C*, uterus simplex. (From Gegenbaur.) *od*, oviduct; *u*, uterus; *v*, vagina.

Thus there are three different types of the female genitalia, in which the vagina is not differentiated (Ornithodelphia), or is double (Marsupialia), or is single and unpaired (Monodelphia). To these correspond three types of development. The Ornithodelphia are oviparous, the others viviparous, but are distinguished by the duration of pregnancy. The eggs of the viviparous forms are so small (about .01 inch) that they have a total, nearly equal segmentation. Such eggs require nourishment from the mother in order to produce an animal with the complicated structure of a mammal. Since in the Didelphia the uterine nourishment is usually very incomplete, the period of pregnancy is very short, in comparison with the Monodelphia, in which a placenta, a complicated apparatus for the nourishment of the young, appears; hence the marsupials, with their small imperfectly formed young, are often called Aplacentalia; the Monodelphia, Placentalia.

All mammals care for the young, this being chiefly or wholly done by the mother, who not only supplies them with milk but protects them in warm if rude nests. Most mammals are monogamous, some polygamous, while in others there is no permanent association of the sexes. The body temperature is constant and ranges from 36° to 41° C. (98° to 106° F.); in Echidna it is only 26° to 34° C. (79° to 83° F.). In most, continual feeding is necessary for existence; from this rule there are a few exceptions, like the bears, marmots, badgers, etc., which hibernate during the winter, taking no food. At this time there is a fall in the temperature due to the diminished metabolism.

Sub Class I. Monotremata (Ornithodelphia, Prototheria).

A few mammals, confined to Australia and New Guinea, divided among the genera *Echidna*, *Proechidna*, and *Ornithorhynchus,* are the only living representatives of the group. They are distinguished from all other mammals by laying eggs about half an inch long, rich in yolk and with soft shells. These undergo in the uterus a discoidal (meroblastic) segmentation and are then incubated by *Ornithorhynchus* in a nest, by *Echidna* in a temporary pouch (marsupium) on the ventral surface of the body. On hatching the young are nourished by the secretion of enormously enlarged sweat glands, which form two large masses to the right and left of the mid-ventral surface, and which must not be confounded with the milk glands (sebaceous) of other mammals. Each opens on a special region of the ventral surface, which is slit-like in *Ornithorhynchus,* a flattened pocket in the others.

Other distinctions from other mammals, which are also points of resemblance to reptiles and birds, are the strong development of the episternum and the extension of the coracoid to the sternum (fig. 648), the termination of the ureters in the urogenital sinus and not in the fundus of the bladder (fig. 653), the existence of a cloaca in both sexes, and the specifically bird-like character of the female sexual organs, in which the large left ovary is alone functional, and uterus and vagina are not differentiated. But with all this it must not be forgotten that the monotremes have the hair, the skull, the urogenital sinus of true mammals, and in the presence of marsupial bones (fig. 655, *Om*) show a close relationship with the marsupials. The upper end of the hyoid is connected directly or by a ligament with the cartilaginous auditory opening, while a scarcely visible external ear occurs. The jaws are toothless and enclosed in horny sheaths, yet in the young of *Ornithorhynchus* there are in each jaw three pairs of multitubercular molars, which are later replaced by four broad horny plates.

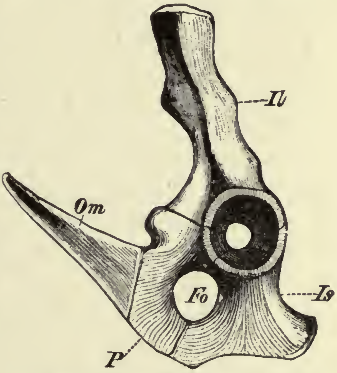


FIG. 655.—Pelvis (left side) of *Ornithorhynchus paradoxus.* (From Wiedersheim.) *Fo*, obturator foramen; *Il*, ilium; *Is*, ischium; *Om*, marsupial bone; *P*, os pubis.

ECHIDNIDÆ. The spiny ant-eaters have the body covered with bristles, snout with a worm-shaped tongue used in catching insects; *Echidna aculeata* of Australia, feet five-toed, with digging claws; *Proechidna* (*Acanthoglossus*) of New Guinea, three-toed. ORNITHORHYNCHIDÆ. The duckbills are toothless, close-haired animals with horny jaws which resemble those of a duck; the five-toed feet with a swimming web especially well developed on the fore feet. *Ornithorhynchus paradoxus* of Australia.

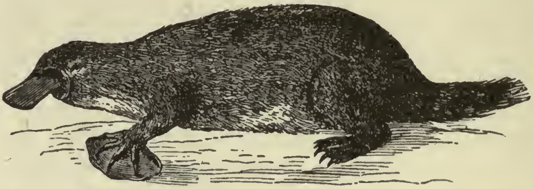


FIG. 656.—*Ornithorhynchus paradoxus*, duckbill. (From Schmarda.)

The male has a spine with a gland on the hind feet which fits in a corresponding pit on the thigh of the female and apparently plays a rôle in copulation.

The oldest fossil mammals are possibly to be regarded as belonging to the monotremes. These appear in the trias and form a group, MULTITUBERCULATA (Allotheria), which is but imperfectly known (*Tritylodon*, *Microlestes*, *Plagiaulax*). Their multitubercular teeth resemble the temporary ones of *Ornithorhynchus*, while there are indications that the coracoid existed as a distinct bone. Less certain are the PROTODONTA (*Dromatherium*, *Microconodon*) of the American Jurassic, of which only the lower jaws are known.

Sub Class II. Marsupialia (*Didelphia*).

These, like the remaining mammals, are viviparous. They have small eggs which undergo a total segmentation in most species, and develop in the maternal uterus, being nourished by a secretion from its walls. In a few species there is a placenta which, in *Perameles*, is allantoic in origin, in *Dasyurus viverrinus* possibly also from the yolk sac. In most species there is no placenta. In all there is insufficient nourishment and the young are born in a very immature condition. They are therefore carried a long time by the mother in the marsupium, a pouch formed by a fold of skin on the posterior ventral surface, into which the nipples open. The ventral surface is supported by the marsupial bones, slender rods articulated, right and left, at the pubic symphysis. Other characteristics of the marsupial skeleton are the inflected posterior angle of the lower jaw (fig. 657, *a*) and the rudimentary replacement of teeth. The milk teeth and molars (first dentition) are as a whole retained, only premolar 3 being replaced by another tooth; but it is in question whether this belongs to the second dentition or is a belated member of the first. The sexual apparatus has already been described (p. 630).

Marsupials are known from the secondary (Jurassic) and tertiary strata of Europe and both Americas. They were apparently then spread over the whole earth, but were crowded out by the placental mammals and persisted only as remnants (*Cœnolestes* and the opossums) in America, but as a richly developed fauna in Australia. In the latter region they continued because here, on account of the early separation of this continent from the rest of the world, no development of Placentalia occurred. The placentals are entirely lacking in Australia with the exception of those introduced by man and such (mice, bats, seals) as easily pass from island to island. In their present habitat, in adaptation to similar conditions they have undergone a development analogous to that of the placentals in other parts of the earth, so that they present groups parallel with the carnivores, rodents, insectivores, and ungulates.

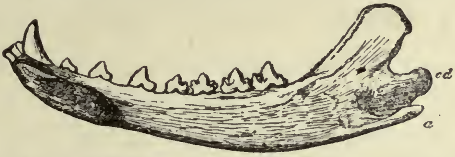


FIG. 657.—Lower jaw of *Thylacinus cynocephalus* (from Flower), showing (*a*) the inflected angle characteristic of marsupials; *cd*, articular surface.

Order I. Polyprotodonta (Zoophaga).

Many marsupials, among them the oldest, have a dentition adapted to animal food. They have numerous incisors (up to five in each half-jaw), strong canines, and sharp-pointed molars (fig. 657). Some in teeth, as well as in body form, resemble the Insectivora, others the carnivores.

The Dasyuridæ are carnivorous: *Dasyurus; Sarcophilus ursinus*, the Tasmanian 'devil,' dangerous to larger mammals; *Thylacinus*, pouched wolf. The PERAMELIDÆ are insectivorous; *Perameles*, bandicoot. The DIDELPHYIDÆ, or opossums, which are confined to America (chiefly South) are more carnivorous in dentition and recall the apes with their opposable thumb. *Didelphys virginiana.**

Order II. Diprotodonta (Phytophaga).

The herbivorous habits are correlated with the degeneration of canines, which usually are lacking in the lower jaw and are at least very small in the upper. There are also only two incisors, of large size, in the lower jaw, while the middle two of the upper are much larger than the one or two lateral which may be present.

The PHASCOLOMYIDÆ are the rodents of the marsupials with one chisel-like incisor in each half of each jaw. *Phascalomys*, wombat. The MACRO-

PODIDÆ, or kangaroos, resemble the ungulates in their large herds on the grassy places. The fore legs being very small, the animals leap with the strong hind legs and tail. *Macropus giganteus.* The PHALANGISTIDÆ have very variable teeth. They resemble in habits the squirrels, *Petaurus* having the same parachute folds as does our flying squirrel. The Diprotodonta contain many fossil forms in Australia and a few in South America. Some of the Australian fossils were very large, *Diprotodon australis* larger than a rhinoceros.

Sub Class III. Placentalia (*Monodelphia*).

The first reason for associating the mammals of the Old World and most of those of the New together as Placentalia is an embryological one, the presence of a placenta. When serosa, amnion, and allantois (p. 553) have developed in the embryo, the vessels of the allantois spread out beneath the serosa and form with this the chorion, which sends small processes or villi into the now highly vascular mucous membrane of the uterus in order to obtain nourishment somewhat as a tree obtains food by its roots. These villi may be distributed over the greater part of the surface (fig. 658), producing the chorion frondosum, or diffuse placenta, which occurs in Cetacea, perissodactyles and many artiodactyles (swine). On the other hand the villi may be restricted to certain places, becoming very strong there. This gives rise to cotyledonary, discoidal, or zonary placentæ. To these correspond portions of the uterine lining which are distinguished from the rest by becoming extremely vascular (uterine placenta). The cotyledonary placenta (fig. 659) consists of many small placentar patches, the cotyledons (most ruminants). In the zonary placenta the villous area takes the shape of a girdle or barrel (carnivores, Sirenia), while the discoidal (other mammals) is, as its name indicates, disc-like.

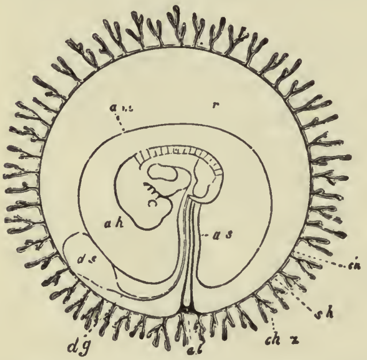


FIG. 658.—Diagram of mammalian embryo with chorion frondosum; *ah*, amniotic cavity; *al*, allantois; *am*, amnion; *as*, umbilical cord; *ch*, chorion; *chz*, chorionic villi; *dg*, yolk stalk; *ds*, yolk sac; *r*, space (extra-embryonic cœlom), between chorion and amnion; *sh*, serosa.

Besides the placental structures the higher mammals are characterized by the disappearance of the cloaca, the unpaired vagina, and absence of marsupial bones and inflected angle of the jaw. The dentition, on the other hand, has undergone a progressive, divergent development, so that the distinctions are much more pronounced than in the marsupials, and hence of importance in differentiating the orders.

Order I. Edentata.

A few families, poor in species, are united under the name Edentata because teeth are absent or, as is more usually the case, are markedly degenerate. Persistent functional incisors are lacking, canines but rarely occur (*Bradypus*); molars may be present, sometimes in great numbers (*Priodon gigas,* the large armadillo, has about a hundred molars), but they are poorly rooted, prismatic, without enamel, and usually monophyodont. Since the aardvark (*Orycteropus*) and *Tatusia* have a heterodont milk dentition in embryonic life in which incisors occur, and fossil edentates (*Entelops*) with complete dentition are known, the absence of a replacement of the teeth is to be explained by degeneration, which may affect other parts, and is to a certain extent the reason for the low position accorded these forms. The great number of sacral vertebræ is striking, being as many as thirteen in some armadillos. The placenta is very variable, being diffuse, discoidal, or zonary in different species. The group is essentially tropical, but one species

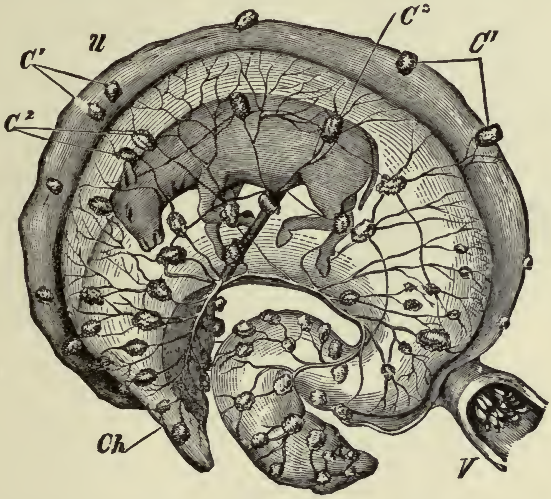


Fig. 659.—Cotyledonary placenta and embryo of cow. (From Balfour, after Colin.) C^1, cotyledons of uterine, C^2, of fœtal placenta; *Ch*, chorion; *U*, uterus; *V*, vagina.

entering the United States. The oldest fossils occur in the Santa Cruz beds of Patagonia (eocene or oligocene).

Sub Order I. NOMARTHRA. Old World edentates. FODIENTIA. Animals with strong digging claws, long tail, and long, vermiform, sticky tongue used in catching ants and other insects. *Orycteropus capensis,* aardvark, with long snout, sparse bristly hair, five small molars, and rudimentary milk dentition. SQUAMATA. Toothless, body covered with overlapping scales. *Manis*, pangolins of Asia and Africa (fig. 660).

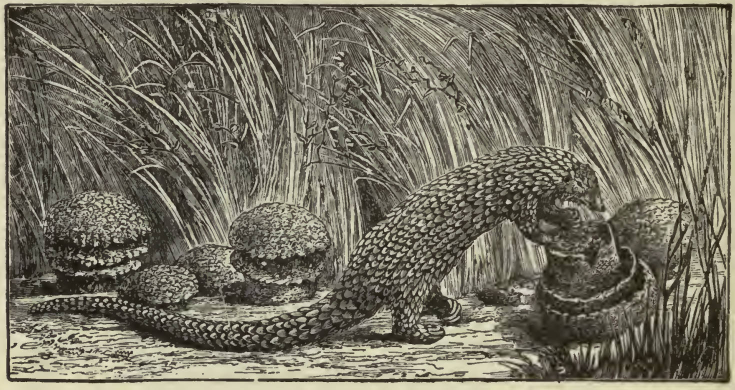


FIG. 660.—*Manis longicaudata*, pangolin. (From Monteiro.)

Sub Order II. XENARTHRA. Edentates of the New World. VERMILINGUIA, ant eaters. Resemble manids in toothless jaws, long ant-catching tongues, and strong digging claws, but are hairy and lack scales. *Myrmecophaga.* TARDIGRADA, sloths. Hairy, head short, rudimentary tail, and few teeth, long strong claws by which they hang back downwards from limbs of trees. *Bradypus tridactylus*, nine cervical vertebræ; *Cholœpus*, six cervicals. Fossils allied are *Megatherium*, as large as an elephant, *Mylodon*, *Megalonyx*, these two extending north to Pennsylvania. LORICATA, armadillos. Body with armor of bony plates, molars numerous; insectivorous. In the extinct GLYPTODONTIDÆ of South America the plates fused to a continuous armor. One species twelve feet long. One species may have occurred in Europe. DASYPODIDÆ; dermal armor in three or more movable transverse plates; nocturnal. Genera based upon the number of bands: *Dasypus*, *Xenurus; Tatusia novemcincta* * enters United States.

Order II. Insectivora.

These primitive forms have a complete dentition, all the different kinds of teeth being present, although they vary in number. The roots are developed early and consequently the teeth are small. Since they end with sharp cusps, adapted for eating insects, they resemble the carnivores, from which they may be distinguished by the rudimentary condition or occasional absence of the canines (*Talpa* $\frac{3}{3}\frac{1}{1}\frac{4}{4}\frac{3}{3}$. many shrews $\frac{4}{2}\frac{1}{0}\frac{2}{1}\frac{3}{3}$). There is great variability in the matter of replacement of teeth; in the shrews, for instance, the milk dentition is suppressed and the second only is functional, while in the hedgehog one incisor and one premolar in each jaw, a second premolar and the canine of the lower jaw function in both dentitions. In many respects the insectivores resemble the rodents: a clavicle is present; there are usually five toes furnished with claws; there is a uterus bicornis, often divided its whole length, and discoidal placenta.

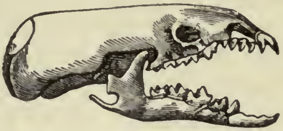


Fig. 661.—Skull of *Sorex*. (From Ludwig-Leunis.)

Aside from the proboscis-like snout the insectivores resemble the rodents in appearance, forming parallel groups to those of that order. The Erinacidæ, or hedgehogs, of the Old World are spined like the porcupines; the Soricidæ, or shrews (*Sorex*,* *Blarina**), are mouse-like, as are the allied Talpidæ, or moles (*Scalops*,* *Condylura*,* star-nosed mole), which burrow in the earth and have the eyes more or less rudimentary. Some authors place here *Galeopithecus* of the East Indies, which has a similar membrane and similar sailing powers as the flying squirrels. It also presents resemblance to the bats and to the lemurs. The earliest known insectivores date from the eocene.

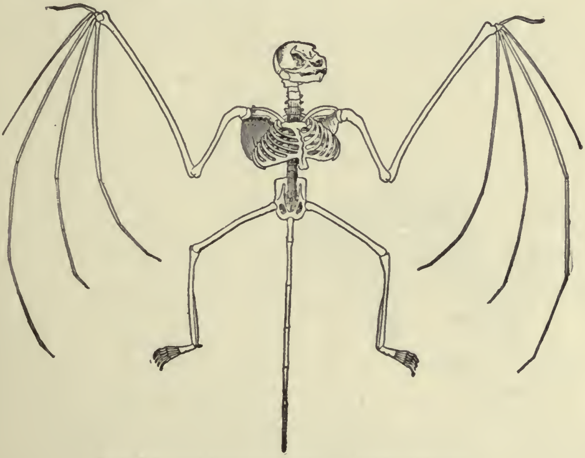


Fig. 662.—Skeleton of bat. (After Brehm.)

Order III. Chiroptera.

The bats are the only mammals which actually fly, and this at once characterizes them. The flying membrane (patagium) is a thin fold of skin, richly supplied with nerves, which begins at the tail, includes the lower extremities to the foot, and extends thence to the fingers, leaving the thumb free. Fingers 2–5 are enormously elongated and support the membrane. Since flight requires strong muscles, the sternum develops a small keel, recalling that of birds, for the attachment of the large pectoral muscle. In connexion with the flying powers the clavicle is strong. The patagium is the seat of a very acute tactile sense, by means of which blinded bats can fly among all kinds of obstacles without disturbing them. The enormous ear conchs and a noticeable nose leaf, widely distributed through the group, also have marked tactile powers. In the pectoral position of the mammary glands and in the discoidal placenta these animals resemble the primates. In temperate regions bats hibernate during the winter. The dentition is variable, often $\frac{2}{3}\frac{1}{1}\frac{3}{3}\frac{3}{3}$. Fossils occur in the eocene.

Sub Order I. MICROCHIROPTERA, with insectivorous dentition, only the thumb of the fore limbs clawed. **Vespertilionidæ**, tail long, no nose leaf; *Vesperugo*,* *Atalapha*.* **Phyllostomidæ**, with nose leaf, tropical America; *Desmodus*, the blood-sucking or vampyre bat.

Sub Order II. MACHROCHIROPTERA (Frugivora), with smooth-crowned molars, claws on thumb and first two fingers. Includes the flying foxes, *Pteropus*, of the East Indies.

Order IV. Rodentia.

The rodents unite great similarity in appearance with a characteristic dentition. The canines are absent, and the molars are separated by a large gap (diastema) from the incisors (fig. 663). The latter are strong, chisel-like, have persistent pulps and grow at the lower end as they are worn away at the cutting edge. Since only the front surface has enamel, wear keeps them constantly sharp. Usually there is but a single incisor, and only in the Duplicidentata is a second present in the upper jaw. The molars are cuspidate or have enamel folds and frequently continue to grow throughout life. Their number is frequently reduced, the formulæ varying between $\frac{2}{1}\frac{0}{0}\frac{3}{2}\frac{3}{3}$ and $\frac{1}{1}\frac{0}{0}\frac{0}{0}\frac{2}{2}$. Many species have an inflected angle of the jaw like that of marsupials. The infraorbital canal is a striking feature in Muridæ and Hystricidæ (fig. 663, *o*), a

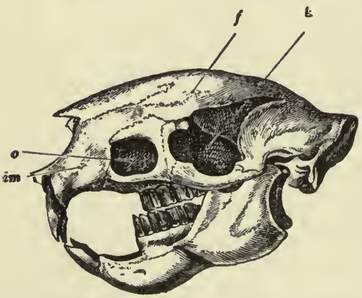


FIG. 663.—Skull of porcupine. (From Schmarda.) *f*, frontal; *im*, premaxillary; *k*, temporal fossa continuous in front with orbit; *o*, infraorbital foramen, enormous on account of the portion of the masseter muscle which passes through it.

large opening in front of the orbit in which a part of the masseter muscle is attached.

The rodents are distinguished from the ungulates, which, like them, are herbivorous, by the usually smaller size, the possession of claws, five toes (sometimes reduced to three), the occurrence usually of a clavicle, and a discoid placenta. The mammæ are inguinal in position and, corresponding to the great fertility, are very numerous. The occurrence of glands with a strong-smelling secretion, which open near the anus, is common. About nine hundred living species are known, occurring in all regions except the Australian. The order appears in the eocene.

Sub Order I. DUPLICIDENTATA (Lagomorpha), two upper incisors, includes the hares, *Lepus*,* and the picas, *Lagomys*.*

Sub Order II. SCIUROMORPHA. The squirrels, SCIURIDÆ, are distinguished by the soft fur and bushy tail. *Sciurus*,* squirrels; *Cynomys*,* prairie dogs; *Sciuropterus*,* flying squirrels. The CASTORIDÆ have soft fur and scaly tail. *Castor fiber*,* beaver of Europe and America.

Sub Order III. MYOMORPHA, rats and mice. *Mus musculus*,* common mouse; *Mus rattus*,* house rat, once abundant but now replaced by the gray rat, *M. decumanus*,* an immigrant from Asia. White rats are albinos of *M. rattus*. *Fiber zibethicus*,* musk rat; *Arvicola*,* field mice.

Sub Order III. HYSTRICOMORPHA. The porcupines (HYSTRICIDÆ) have spines; the Old World forms, *Hystrix*, are terrestrial, ours (*Erethyzon*) arboreal. The CAVIIDÆ of South America have hoof-like claws. *Cavia cobaya*, guinea pig. *Hydrochœrus*, capybara, the largest existing rodent.

Order V. Ungulata.

Under the heading of Ungulata, or hoofed animals, are here included two groups of living animals in which the body weight is supported on hoofs on the tips of the toes, and which are sharply marked off from other forms. If, however, the fossils are included, the limits of the group must be extended so that it includes the elephants and conies of the existing fauna as well as several extinct forms, for these so interlock and intergrade that sharp lines cannot be drawn.

The ungulates, which arise from common ancestors, the Condylarthra, the representatives of which occur in the eocene of America (*Phenacodon*), are preeminently herbivorous; the canines are rarely well developed, the molars numerous and adapted to grinding the food, more or less flattened and frequently with folded enamel. The mammæ are inguinal, the uterus bicornuate, and the placenta either diffuse or (most ruminants) cotyledonary (fig. 659). The legs are exclusively locomotor structures and, to permit freer motion, the clavicles are absent; the feet touch but the tips of the toes, enclosed in hoofs, to the ground (unguligrade). Since the metacarpals and metatarsals are greatly elongate, the wrist and ankle are raised high from the ground so that they are frequently confounded with elbow and knee. With this exclusively supporting character of the limbs there is the same tendency to reduction and fusion of bones which was noticed in birds (p. 606). There is a constant increase in the development of radius and tibia to the chief supports of the body, the fibula becoming rudimentary, the ulna being developed sometimes throughout its whole extent, sometimes only in its upper part, which serves for the attachment of muscles (olecranon), and is more or less fused with the radius. The same tendency to simplification prevails in the feet, but is expressed differently in the odd-toed (perissodactyle) and even-toed (artiodactyle) forms. In the Perissodactyla the axis of pressure passes through the middle toe (fig. 664, *A–C*, III), while the other toes disappear symmetrically around this. Since the first toe is early lost, toe V is next to disappear (*B*), and then toes II and IV (*C*), so that at last there remain only the skeleton and hoof of the middle toe (horse), the rudiments of toes II and IV persisting as the small splint bones.

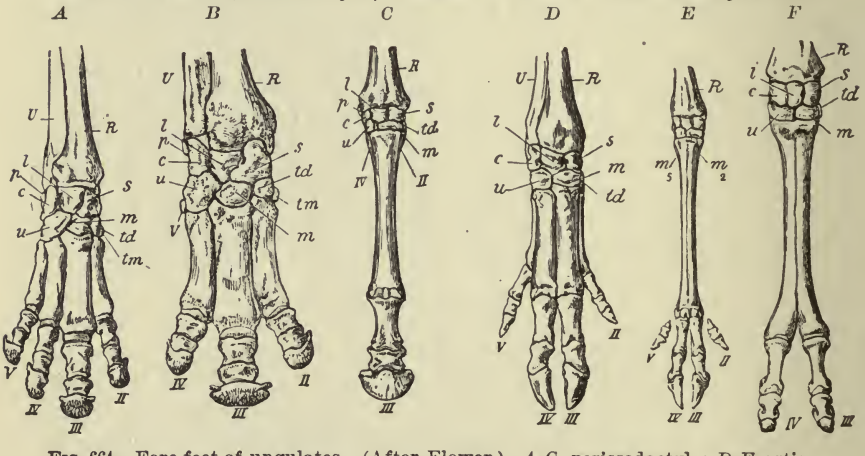


Fig. 664.—Fore feet of ungulates. (After Flower.) *A–C*, perissodactyle; *D–F*, artiodactyle. *A*, tapir; *B*, rhinoceros; *C*, horse; *D*, pig; *E*, deer; *F*, camel. *c*, triquetrum (ulnare); *l*, lunatum (intermedium); *m*, capitatum; m^2–m^5, rudiments of metacarpals II and V; *p*, pisiforme; *R*, radius; *s*, scaphoid (radiale); *td*, trapezoid; *tm*, trapezium; *U*, ulna; *u*, hamatum; II–V, digits.

In the Artiodactyla the axis of pressure falls between toes III and IV (fig. 664, *D*), which both unite in supporting the body and are equally developed and frequently fuse, at least so far as the metacarpals are concerned (*E*, *F*). The figures *D–F* show

how the other digits disappear, digit I being lost still earlier. Since the weight of the body rests more upon the hind legs than upon the front ones, the former are the first to become modified. Since we are able, by using abundant paleontological material, to follow in detail the lines of descent of both artiodactyles and perissodactyles, the conclusion is certain that these form diverging series, distinct from the beginning. In each series most of the common characters enumerated above have been independently acquired so that the uniformity in appearance of the various groups of ungulates is in great part the result of convergence. The discussion of the fossils will be given under a separate head.

Sub Order I. PERISSODACTYLA (Solidungula). The dentition is peculiar in having molars and premolars (with more or less pronounced enamel folds) of equal size; a second character is the predominant development of the middle toe, the others in the three existing families reduced to different degrees. TAPIRIDÆ, fore feet four-toed, hind feet three-toed; teeth $\frac{3143}{3133}$; nose elongate into a proboscis. *Tapirus*, tapirs, tropical America and India. RHINOCEROTIDÆ, three toes on all feet, teeth $\frac{2043}{2043}$; one or two horns on the nasal bones, these without skeleton; skin thick, hairless, hence these were formerly united with elephants as Pachydermata. *Rhinoceros*, a single horn, India; *Ceratorhinus* (Asia), *Atelodus* (Africa), have two horns. EQUIDÆ, a single functional toe, toes II and IV forming splint bones (fig. 664, *c*); teeth $\frac{3133}{3133}$; *Equus caballus*,* horse, a native of Asia; *E. asinus*, ass; *E. zebra*. Hybrids between jackass and mare are called mules; between stallion and she-ass, hinnies.

Sub Order II. ARTIODACTYLA. Besides the features of the feet, these forms have the premolars, three or four in number, smaller than the molars. The species are much more numerous than the perissodactyles and may be divided into three sections. Section I, NON-RUMINANTIA (Bunodontia); omnivorous and have correspondingly a bunodont dentition, $\frac{2-3143}{1-3143}$, the canines frequently developed into tusks; the stomach is usually simple, but is occasionally divided into three chambers (*Dicotyles*, *Hippopotamus*), although rumination does not occur. The leg skeleton is little modified (fig. 664, *D*), ulna and fibula not being reduced, and metacarpals and metatarsals separate. HIPPOPOTAMIDÆ; all four toes reach the ground; skin thick ('pachyderm'), body heavy; living species all African. *Hippopotamus*. SUIDÆ; two functional toes, skin with bristles, snout proboscis-like. *Sus scrofa*, swine; *Dicotyles*,* peccaries of warmer America.

Section II. RUMINANTIA (Pecora); teeth and stomach are adapted to the exclusively herbivorous diet. The stomach (fig. 665) is divided into two portions, each again subdivided. The first of these, the rumen, or paunch (*ru*), receives the food as it is eaten; then at a time of quiet it is regurgitated into the mouth and ground by the molars ('chewing the cud'). It then passes back, this time into the second division, the honeycomb, or reticulum (*re*), thence to the manyplies or omasum (*o*), and lastly to the abomasum, or true stomach (*a*). Usually not only the canines but the incisors of the upper jaw are degenerate, while the incisors of the lower jaw are strong and the canines have taken the form and position of incisors. The molars are selenodont (have crescent-shaped cusps). With few exceptions they are of large size and many bear horns on the frontal bones. These are larger in the males and may occur exclusively in that sex. In the simplest case (giraffes) these are cones of horn free from the frontals and covered with skin. In others (Cavicornia) the horn cores fuse secondarily with the frontals and are covered with a firm sheath of horn. Lastly, the horns are outgrowths of the frontal bone, in which usually the outer coats are lost and only the bone projects freely (antlers). These are shed yearly, the new antler which takes its place being larger and consisting of a larger number of branches or tines, thus constituting an index of age (Cervicornia). CAMELOPARDALIDÆ (Devexa), giraffes, long-legged forms (two genera) from Africa with persistent horns; teeth $\frac{0\,0\,3\,3}{3\,1\,3\,3}$, *Giraffa*. CERVIDÆ, deer, with deciduous horns in the male. *Cervus*,* common deer; *Alces*,* moose; *Rangifer*,* reindeer; MOSCHIDÆ, horns lacking, males with enlarged upper canines and with a musk gland (the source of the familiar perfume) on the ventral surface; *Moschus*, central Asia. The TRAGULIDÆ, primitive Asiatic and African forms, includes the chevrotain, *Tragulus javanicus*, the smallest living ungulate. The CAVICORNIA include a large number of forms, some of great economic importance; teeth $\frac{0\,0\,3\,3}{3\,1\,3\,3}$. BOVIDÆ: *Bos taurus*, domestic cattle, probably descended from three distinct stocks (*B. primigenius*, the aurochs, *B. longifrons* and *B. frontosus*); *Bison*,* including *B. europeus*, the bison proper, and *B. americanus** our ‘buffalo,’ so near extinction; *Bubalus*, the true buffalo of the Old World. OVIDÆ: *Ovis aries*, sheep; *O. montana*,* big horn; *Capra hircus*, goat; *Ovibos moschatus*,* musk ox. ANTILOPIDÆ: including a host of Old World forms (*Antilope*, *Gazella*, *Rupicapra tragus*, the chamois, etc.) and *Antilocapra americana*,*

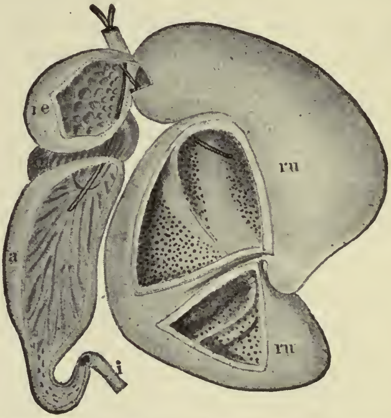


FIG. 665.—Stomach of sheep. (After Carus and Otto.) *a*, abomasum (true stomach); *o*, omasum (manyplies); *re*, reticulum (honeycomb); *ru*, rumen (paunch).

the prong horn, which sheds its horns, and *Hoploceras montanus*,* the Rocky mountain sheep.

Section III. TYLOPODA, stomach without manyplies, no frontal horns, diffuse placenta. *Camelus*, the camels of the Old World; *C. dromedarius*, one hump; *C. bactrianus*, two humps. *Auchenia lama*, *A. alpaca* of South America.

Paleontology of the Ungulata.

Extensive paleontological material, especially from the tertiary rocks of our western states, has cleared up many lines of ungulate descent and has rendered it probable that the CONDYLARTHRA of the eocene, with five-toed plantigrade feet, well-developed ulna and fibula, and an omnivorous dentition, formed the stock from which descended the artiodactyles and perissodactyles, and possibly carnivores and primates as well, the ungulate line extending through the Amblypoda. From one group of these (the PHENACODONTIDÆ) the lines of rhinoceros and tapir have come, and in an almost complete series we know the ancestry of the horse. *Hyracotherium* (*Eohippus*) and *Orohippus* of the eocene had the fore feet four-toed (fig. 666, *1*); *Palæotherium* and *Mesohippus* (*2*) of the lower miocene and *Miohippus* of the later miocene were three-toed, while *Meryhippus* and *Hipparion* (*Pliohippus*, *4*) of the pliocene were near the horse in tooth structure. The single-toed horses appeared in the pleistocene with *Pliohippus* (*5*) and then *Equus* itself (*6*). It is a peculiar fact that the horse entirely died out in America, although the chief part of its history was enacted here.

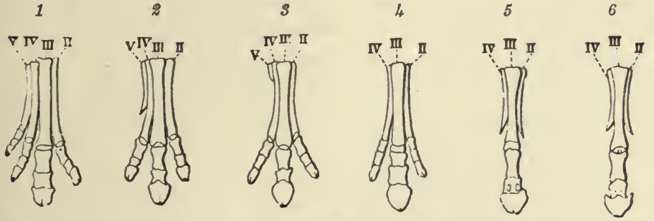


FIG. 666.—Evolution of fore foot of horse. (From Wiedersheim.) *1*, *Orohippus* (eocene); *2*, *Mesohippus* (lower miocene); *3*, *Miohippus* (miocene); *4*, *Protohippus* (upper pliocene); *5*, *Pliohippus* (pleistocene); *6*, *Equus*.

The AMBLYPODA, mentioned above, were semi-plantigrade pentadactyle forms, appearing in the lowest eocene, and reaching, in *Uintatherium* (*Dinocerus*) an elephantine size. The TOXODONTIA of the South American tertiaries combined perissodactyle, rodent, hyracoid, and proboscidian features, while the TILLODONTIA of the eocene recall both carnivores and rodents.

Order VI. Proboscidia.

The elephants and their allies, with their hoofs and herbivorous dentition, are closely related to the ungulates. They are characterized by their thick skin ('pachyderm'), the large, massive, five-toed legs, and especially by the nose drawn out into a long proboscis with a finger-like process at the tip, lastly by the dentition. Canines are entirely lacking, but the incisors of the upper jaw have pulps and therefore continue to grow throughout life, forming the well-known tusks. In the living elephants there are but a single pair of tusks, but in some extinct *Mastodons* there were a second smaller pair in the lower jaw, while in *Dinotherium* only the lower incisors were developed, these projecting downwards. The molars (in *Mastodon* and *Dinotherium* with normal replacement and cusps) consist of numerous plates of enamel and dentine united by cement, and undergo a lateral displacement. Of the three large molars and premolars only one at a time is functional (fig. 667, *1*); when worn out the next one behind (*2*) takes its place. Further features are a uterus bicornis, a zonary placenta, and two pectoral mammæ.

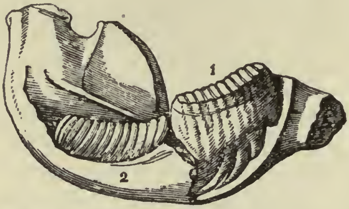


FIG. 667.—Inside of left lower jaw of *Elephas indicus*, the alveoli opened. (After Owen.) *1*, functional molar; *2*, its successor.

ELEPHANTIDÆ: *Elephas indicus*, small ears; *E. africanus*, large ears. *E. primigenius*, mammoth, in the pleistocene; specimens found frozen in ice in Siberia have close woolly hair, in some places three feet long. *Mastodon*, with tuberculate teeth, range from miocene through the pliocene. DINOTHERIDÆ, only lower incisors; *Dinotherium*, Old World miocene.

Order VII. Hyracoidea.

The single genus *Hyrax*, including species from western Asia and Africa, with four-toed front feet, hind feet with three toes, the digits with nails, the placenta zonary, and the dentition $\frac{1}{2}\frac{0}{0}\frac{4}{4}\frac{3}{3}$, forms this group, no fossils being known. *Hyrax syriacus* is supposed to be the 'coney' of the Bible.

Order VIII. Sirenia.

This order consists of a few aquatic mammals which are whale-like in form, with the fore limbs fin-like, the hind legs lacking, and a horizontal caudal fin. They live in shallow seas or in the mouths of rivers, where they feed on the tang, which they chew with jaws covered with horny plates. The teeth (in the fossil *Prorostomus* $\frac{3}{2}\frac{1}{1}\frac{4}{4}\frac{4}{4}$) are reduced or entirely lacking. The fore legs are pentadactyle and often have rudimentary nails and always a flexible elbow. The two pectoral mammæ have possibly caused these animals to furnish the germ of truth in the mermaid myth. *Manatus americanus*,* the manatee, six cervical vertebræ, eight to ten molars; *Halicore dugong*, Indo-Pacific; *Rhytina stelleri* of the northern Pacific, exterminated in 1768.

Order IX. Cetacea.

In external form the whales resemble the sirenians, a result of an aquatic life, but the resemblance ends here. The whales are so fish-like that they are commonly included by the laity in that group, and every one speaks of the whale fishery. Head and trunk are scarcely distinguished, the cervical vertebræ being very short and more or less completely fused. The hinder limbs are absent, and of the pelvic girdle only a small ilium remains, and no sacral vertebræ are developed. The caudal fin is two-lobed and differs from that of a fish in being horizontally flattened; the skin is thick and is sparsely haired or completely naked, in some hair being lacking even in the embryo. Most of the species inhabit the high seas, *Inia boliviensis* and *Platanista gangetica* occur in rivers.

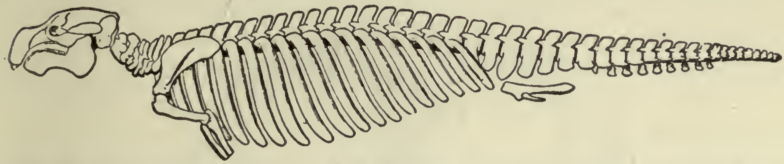


FIG. 668.—Restoration of skeleton of *Halitherium*, an extinct sirenian. (After Miss Woodward.)

The fore limbs are modified into flippers, the bones of which are of nearly equal size and are jointed only at the shoulder. A dorsal fin ('fin backs') occurs in some. The lack of hair is compensated by the thick layer of subcutaneous fat (blubber) which, like the fat penetrating the spongy bones, tends to lessen the specific gravity. In order that the animals may breathe while feeding, the larynx is prolonged into a tube which extends up through the pharynx to the choanæ, from which the nostrils extend directly upwards to the single (Denticetes) or paired (Mysticetes) external opening. Since the air driven out with great force contains much moisture and this is condensed on contact with the cooler external air, the impression was natural that the animals in 'blowing' spouted water. Since the olfactory membrane is degenerate and the olfactory lobes are reduced, the nose is an organ of respiration only.

The eyes are small, external ears are lacking, the mammæ are close to the sexual opening. The teeth are either present in large numbers, similar and conical, and, since the second dentition is rudimentary, are monophyodont (Denticetæ) or they are outlined early and then resorbed and replaced by plates of baleen (Mysticetæ). This is composed of large horny plates (whalebone) in large animals a dozen feet long (fig. 669, *w*), of which several hundred are arranged in close succession extending inward to the tongue. They correspond to the transverse palatal folds which occur in other mammals. As they are fringed on the inner edges they form a strainer which retains the small marine animals (plankton, *Cetochilus septentrionalis*, a copepod, and *Clione borealis*, a pteropod) on which these whales feed. The œsophagus is too narrow for the passage of much larger animals.

The origin of the whales is one of the unsolved problems. That they came from some terrestrial, quadrupedal forms is beyond question, and the little evidence would seem to point to an ungulate or a carnivore ancestry. It is possible that the toothed and whalebone whales may have had different ancestries, and their resemblances may be the result of convergence.

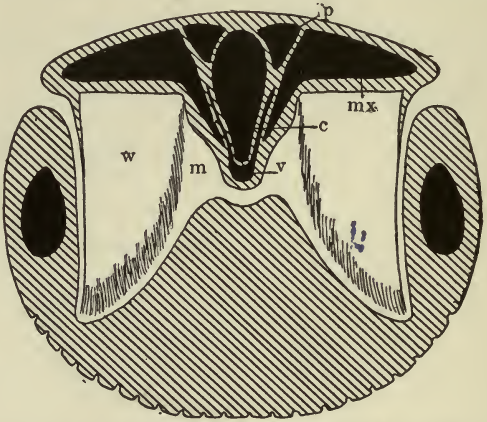


Fig. 669.—Section through jaws of whalebone whale. (After Delage.) *c*, septum of nose; *m*, mouth cavity; *mx*, maxillary bone; *p*, premaxillary (hinder end); *v*, vomer; *w*, baleen.

Sub Order I. ZEUGLODONTA. Extinct (eocene) forms with heterodont dentition, the posterior teeth two-rooted.

Sub Order II. DENTICETÆ, toothed whales, carnivorous, some having but two teeth. *Delphinus*, dolphins; *Globiocephalus*,* black fish; *Monodon*, narwal, with, in the male, a long maxillary tusk (possible origin of the 'unicorn'). *Physeter macrocephalus*, sperm whale, pursued for the spermaceti, an oily mass situated in the 'chair' between the cranium and the snout, as well as for ambergris, formed in the intestines.

Sub Order III. MYSTACETI, whalebone whales, with baleen. *Balænoptera*,* rorquals and fin backs. *B. sibbaldi*,* the largest whale, reaching a length of eighty-five feet. *Balæna*, right whale.

Order X. Carnivora.

The carnivores live chiefly on the flesh and blood of other vertebrates, which they catch by craft, by coursing, or by pouncing upon them, overpowering their prey by their sharp claws and cutting teeth. With this mode of life correspond the high development of the brain (fig. 649, *B*) and sense organs, as well as structure of teeth and claws. Since this predaceous character increases within the order from the bears to the cats, and again tends to disappear in the aquatic species, there are few constant characters, but a great variation in structure. In interest of greater mobility the clavicle is reduced or lost, ulna and radius well developed. In the structure of the feet there is a gradual transition from the plantigrade bears, in which the whole sole of hand and foot rest upon the ground, to the digitigrade cats, which tread on the tips of the toes. In the latter the claws, which occur in all carnivores, are kept from injury, when not in use, by being retracted by an elastic ligament into pockets on the penult joint, from which they are extended by strong muscles. In dentition (fig. 650) the striking features are the almost constantly three incisors, and the great size of the canines; the molars, on the other hand, vary with the different families, the cusps assuming more of the shearing character (secodont teeth). The last premolar of the upper jaw and the first molar of the lower jaw become carnassial teeth (sectorial teeth), and acquire a dominating position in the jaw, while the others become smaller and tend to disappear at either end of the series. Further characters are the possession of a penis bone in the males, the abdominal position of the milk glands and the uterus bicornis in the females; the placenta is zonary. Anal glands, furnishing a strong, even offensive smelling secretion, are of wide occurrence.

Sub Order I. FISSIPEDIA. These are the typical members of the order and are preeminently terrestrial animals with well-developed toes usually cleft to the base. The number of digits is frequently five on all feet, but is often reduced to four on the hind feet (Felidæ, Canidæ), rarely on the fore feet (Hyænidæ); but in these cases, as in the domestic dog, the reduced first toe may bear a claw. URSIDÆ, plantigrade; *Ursus*,* bears; *Procyon lotor*,* raccoon. MUSTELIDÆ; many species of *Mustela* * and *Putorius*,* which include minks, martens, sable, ermines, and weasels, are valuable for their fur; *Lutra*,* otter; *Enhydris*,* sea otter; *Mephitis*,* skunk; *Taxidea*,* badger; *Gulo*,* glutton; anal glands common in this family. Fossils (*Arctotherium*, etc.) connect the bears and the CANIDÆ with five toes in front, four behind, claws not retractile; which includes in the genus *Canis* * dogs, foxes, and wolves. The FELIDÆ have toes as in the dogs, but with retractile claws. *Felis domestica*, our domestic cat. *F. leo*, lion; *F. tigris*, tiger; *F. concolor*,* puma or cougar. HYÆNIDÆ, all feet four-toed; *Hyæna* of Africa.

Sub Order II. PINNIPEDIA. These are aquatic carnivores with the limbs flattened to broad flippers, the five toes long and webbed, the nails frequently rudimentary; the dentition differs from that of the terrestrial forms in the similarity of molars and premolars (absence of carnassial);

the milk dentition degenerates early, without being functional. PHOCIDÆ, seals, without external ears; *Phoca vitulina,** harbor seal. OTARIIDÆ, with external ears; *Otaria,** sea lions; *Callorhinus ursinus*, fur seal of Alaska. TRICHECHIDÆ; incisors reduced, upper canines developed into large tusks; *Trichechus*, walrus.

The first carnivores appear in the eocene in the order CREODONTA, plantigrade forms with slightly differentiated dentition (no carnassial); they present marked resemblances to marsupials, insectivores, as well as to the Condylarthra, the ancestral ungulates. True carnivores appear in the upper eocene and become abundant in the miocene.

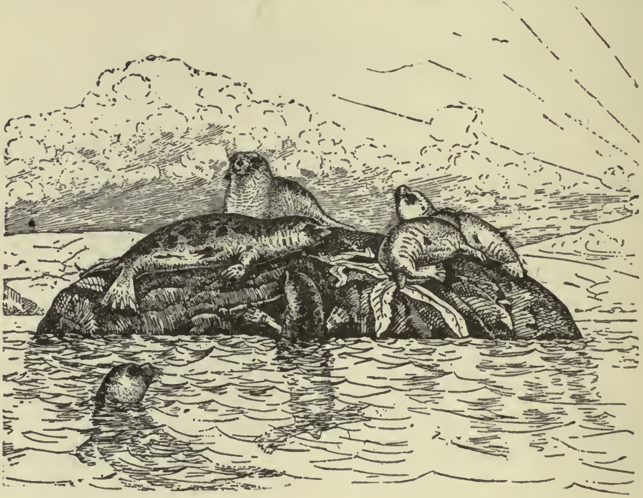


FIG. 670.—*Phoca vitulina*, harbor seal. (After Elliott.)

Order XI. Prosimiæ.

Linné united with the true apes a small group of animals known as lemurs (from India and the adjacent islands, and especially from Africa), because of similarity in body form and climbing habits, because they had grasping hands and feet (opposable thumb and great toe), and at least frequently nails on some of the toes. To-day many set them aside as a separate order on account of their lower organization. They have a less-developed cerebrum, uterus bicornis, and a diffuse placenta. Further peculiarities are the peculiar and variable dentition (*Chiromys* $\frac{1}{1}\frac{0}{0}\frac{1}{0}\frac{3}{3}$, *Lemur* $\frac{2}{2}\frac{1}{1}\frac{3}{3}\frac{3}{3}$) and the presence of claws, which always occur on the second and frequently on the third finger of the hind feet, and in *Chiromys* replace the nails on all the digits of all the feet except the great toe. Their nocturnal habits have resulted in large eyes, which give these animals a most striking appearance. A distinction from the primates is the connexion of orbital and temporal cavities beneath the osseous postorbital ring. Usually there are a pair of pectoral mammæ, to which are added in many species a pair in the abdominal or inguinal region, the latter alone occurring in *Chiromys*.

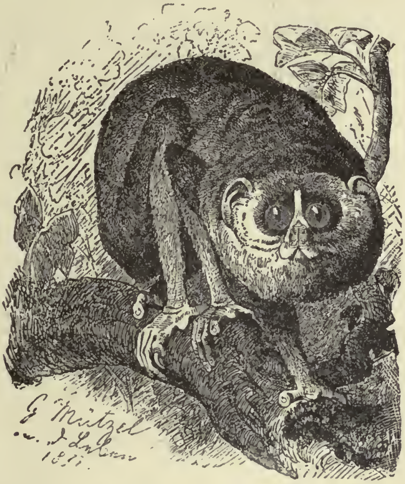


FIG. 671.—*Stenops gracilis*, slender loris. (From Brehm.)

CHIROMYIDÆ, digits long, all except the great toe with claws; *Chiromys madagascarensis*, aye-aye. TARSIIDÆ, second and third hind toes clawed. *Tarsius spectrum* of the East Indies differs from all Prosimiæ in having the orbits closed and a discoidal placenta like that of man. LEMURIDÆ, second hind toe alone clawed. *Lemur; Stenops*, loris. The old tertiary PACHYLEMURIDÆ and ANAPTOMORPHIDÆ are close to the most primitive mammals and to the creodonts and insectivores. The GALEOPITHECIDÆ (p. 637) are often referred here.

Order XII. Primates.

The most highly organized mammals, the monkeys, apes, and man, are united in a single order because among them there is a great agreement in features of classificatory value. If we here, as elsewhere, ignore grades of intelligence and regard alone greater or lesser anatomical resemblances, we are forced to the conclusion that the anthropoid apes are much closer to man than to the lower monkeys.

The primates have in common nails on all the fingers and toes (except the Hapalidæ), orbits separated from the temporal fossæ by a bony wall, and a cerebrum which covers the other parts of the brain (fig. 649, *c*). They have a single pair of pectoral mammæ, uterus simplex, and a discoidal placenta. The dentition is essentially the same throughout; in the Platyrrhinæ $\frac{2\,1\,3\,3}{2\,1\,3\,3}$, in the Hapalidæ $\frac{2\,1\,3\,2}{2\,1\,3\,2}$, in the Catarrhinæ and in man $\frac{2\,1\,2\,3}{2\,1\,2\,3}$. Yet there is a tendency to variation, since in the chimpanzee and in man the third molar (wisdom tooth) is in process of degeneration, while in the orang a fourth molar often occurs. In all the molars are bunodont.

The skeleton of the hand and foot has played an important rôle in classification. As in the lemurs and opossums, the thumb and great toe can be opposed to the other digits, so that an ape can grasp objects with either hand or foot. In man this opposability of the thumb is increased, but that of the great toe, in consequence of the upright position, is only retained to a slight degree by children and primitive people. On this peculiarity rest the names often given of Bimana, for man, and Quadrumana, for the apes and monkeys. In contradiction of this it must be emphasized that the apes do not have a hand, but rather a grasping foot, on the hinder extremities. In the grasping foot (fig. 672) are the same bones, similarly arranged and of about the same shape as in the foot of man, while the musculature is essentially the same. On the other

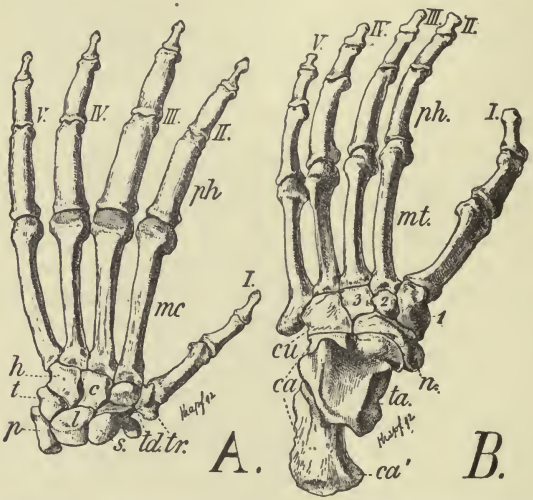


FIG. 672.—Hand and foot of gorilla. *c*, capitatum; *ca*, calcaneus; *cu*, cuboid; *h*, hamatum; *l*, lunatum; *mc*, metacarpals; *mt*, metatarsals; *n*, naviculare; *p*, pisiforme; *ph*, phalanges; *s*, scaphoid; *t*, triquetrum; *ta*, talus; *td*, trapezoid; *tr*, trapezium; *I–V*, digits; *1–3*, cuneiformia.

INDEX.

Aard vark, 636
Abalone, 379
Abdominal cavity, 546
Abdominales, 562
Abdominal fin, 562
Abdominalia, 426
Abducens nerve, 536
Abomasum, 642
Acantharia, 196
Acanthia, 489
Acanthias, 569, 571
Acanthiidæ, 489
Acanthin, 195
Acanthobdella, 318
Acanthoderus, 48
Acanthobothrium, 286
Acanthocephala, 304
Acanthocotyle, 274
Acanthodes, 572
Acanthodidæ, 572
Acanthoglossus, 632
Acanthometra, 194
Acanthophracta, 196
Acanthopteri, 574, 577
Acanthopterygii, 577
Acaridæ, 454
Acarina, 453
Accessory nerve, 536
Accessory tissue, 99
Accessory yolk, 80
Accipiter, 617
Acephala, 358
Acerata, 442
Acetabula, 280
Achæta, 317
Achatina, 383
Achoreutes, 477
Achromatin, 65
Achtheres, 36, 422
Aciculum, 308
Acineta, 212
Acinetaria, 212
Acinous glands, 77
Acipenser, 573
Acipenseridæ, 573
Acmæa, 378
Acmæidæ, 378
Acœla, 271
Acontia, 253
Acorn barnacle, 423
Acrania, 502
Acraspedia, 246
Acraspedota, 246
Acridiidæ, 481
Acridium, 481
Acris, 588
Acrodont teeth, 599
Actinaria, 259
Actinian, section of, 136
Actinophrys, 191, 192
Actinopoda, 349
Actinosphærium, 190, 192
Actinotrichia, 527
Actinotrocha, 325
Actinozoa, 251
Aculeata, 486
Aculeus, 472, 476
Acustic nerve, 536
Adambulacral plate, 335
Adamsia, 254
Adhesive cells, 264
Adipose fin, 576
Adoral band, 209
Adradius, 246
Ægа, 441, 442
Ægina, 242
Æolidæ, 382
Æolidia, 382

Æpiornis, 613
Æquoria, 240, 242
Æschna, 479
Æsthetes, 357
Æthalium, 199
Aftershaft, 603
Agalmia, 244
Agamidæ, 599
Agassiz, 21
Agelacrinoidea, 342
Agelacrinus, 342
Agkistrodon, 601
Aglaophenia, 242
Aglossa, 588
Aglypha, 601
Agnatha, 555
Agrion, 479
Air bladder, 567
Air pipes, 609
Air sacs of birds, 608
Alæ, 466
Alæ cordis, 470
Alauda, 616
Alaudidæ, 616
Albatross, 615
Albertus Magnus, 9
Alca, 615
Alcedinidæ, 616
Alces, 642
Alcidæ, 615
Alciopidæ, 313
Alcippe, 424
Alcyonaria, 258
Alcyonidæ, 259
Alcyonidium, 324
Alcyonium, 255, 259
Aletia, 495
Alima, 429
Alimentary tract of vertebrates, 546
Alisphenoid bone, 522
Allantoidea, 553
Allantois, 553
Alligator, 602
Alligator turtle, 596
Allobophora, 316
Alloposus, 395
Allotheria, 632
Alosophila, 494
Alpaca, 643
Alpheus, 434
Alternation of generations, 144, 512
Altrices, 612
Alula, 604
Alveolar duct, 548
Alveoli, 625
Alveolus, 548
Alytes, 585
Amaroucium, 510
Ambergris, 646
Amblyopsidæ, 576
Amblypoda, 643
Amblystoma, 587
Amblystoma, larva of, 36
Ambulacra, 331
Ambulacral grooves, 335
Ambulacral plates, 335
Ambulacral system, 122, 330
Ambulacral vessels, 331
Ametabolous, 473
Amia, 574
Amia, tail of, 41
Amicula, 357
Amiidæ, 574
Ammocœtes, 557
Ammonitidæ, 394
Amnion, 472, 553
Amniota, 553, 588
Amœba, 61, 62, 187, 189
Amœbina, 189
Amœboid motion, 187
Amphacanthe, 574
Amphiaster, 70
Amphibia, 580
Amphibiotica, 479
Amphicœle, 518
Amphicœlias, 596
Amphidiscs, 227
Amphigony, 142
Amphilina, 286
Amphineura, 356
Amphioxus, 502, 504
Amphioxus, cleavage of, 151
Amphioxus, gastrula of, 156
Amphiphorus, 291
Amphipoda, 438
Amphisbæna, 599

Amphistomum, 278
Amphithoe, 428
Amphitrite, 312, 313
Amphiuma, 585, 587
Amphiura, 338
Amphoridæ, 342
Ampullaridæ, 380
Ampullæ, 223, 331, 542
Amyda, 596
Anabrus, 481
Anacanthini, 577
Anaconda, 601
Anal glands, 106
Anal fin, 526, 562
Anallantoidia, 553, 555
Analogy, 14, 100
Anamnia, 553, 555
Anaplocephalus, 287
Anaptomorphidæ, 649
Anas, 615
Anaspides, 437
Anatomy, 57, 58
Anatomy, comparative, 2
Anaxial form, 135
Androctonus, 400
Anelasma, 423, 424
Angiostoma, 601
Anguillidæ, 576
Anguillula, 300
Anguillulidæ, 300
Anguis, 599
Angulare, 582
Animal morphology, 57
Animal organs, 101. 121
Animal pole, 147, 151
Animals and plants, 171
Anisomyaria, 367
Anisopoda, 442
Annelida, 305
Annulata, 599
Anodonta, 361, 367
Anolis, 599
Anomodontia, 594
Anopheles, 217, 492
Anser, 615
Anseriformes, 615
Antarctic province, 178
Ant eaters, 636
Antedon, 339, 342
Antenna, 401, 410, 430, 463
Antennal gland, 411
Antennulæ, 430
Antheomorpha, 251
Anthomastus, 259
Anthomedusæ, 239, 241
Anthomyia, 492
Anthozoa, 251
Anthropinæ, 651
Anthropoidæ, 651
Anthropopithecus, 652
Antilocapra, 642
Antilope, 642
Antilopidæ, 642
Antimeres, 137
Antipatharia, 259
Antipathes, 259
Antlers, 642
Ant lion, 481, 483
Antrostomus, 616
Antrum of Highmore, 539
Ants, 487
Ants, white, 478
Anura, 588
Anurida, 477
Aorta, 548
Aorta ascendens, 504, 549
Aorta, descendens, 504
Apes, 651
Aphaniptera, 493
Aphidæ, 490
Aphrodite, 313
Apiariæ, 487
Apical plate, 306
Apis, 487
Aplacophora, 358
Aplysia, 381
Aplysilla, 226
Aplysina. 224, 226
Apoda, 349, 425, 587
Apodidæ, 416
Apophysis, 517
Aporosa, 260
Appendicularia, 506
Aprophora, 489
Aptenodytes, 615
Aptera, 491

Apteria, 604
Apteryges, 613
Apterygota, 477
Apteryx, 613
Apus, 416
Aquatic faunæ, 179
Aqueduct of Sylvius, 534
Aqueous humor, 131
Aquila, 617
Arachnida, 444
Araneina, 451
Arbacia, 345
Arcella, 198
Archæan era, 180
Archæopteryx, 33, 612
Archegony, 139
Archenteron, 103, 104, 156
Archianellidæ, 313
Archigetis, 286
Archiptera, 477
Archipterygium, 529
Architeuthes, 384, 395
Arcidæ, 367
Arcifera, 588
Arctic province, 178
Arctogæa, 177
Arctotherium, 647
Arcyria, 199
Ardea, 615
Arenicolidæ, 313
Areolar connective tissue, 85
Argas, 454
Argina, 367
Argiope, 327, 453
Argonauta, 392, 395
Argonautidæ, 395
Argulidæ, 422
Argulus, 421, 422
Ariolimax, 383
Arion, 383
Arista, 493
Aristotle, 7
Aristotle's lantern, 345
Armadillidium, 442
Armadillo, 636
Armata, 317
Army worm, 495
Artemia, 416
Arterial arches, 549
Arteries, 112
Arthrodira, 579
Arthrogastrida, 447
Arthropoda, 398
Arthrostraca, 438
Articular bone, 525
Articular process, 519
Articulata, 342, 398
Artificial impregnation, 147
Artificial selection, 43
Artiodactyla, 640, 641
Arvicola, 639
Ascalabotæ, 598
Ascaridæ, 301
Ascaris, 145, 299
Ascaris, fertilization in, 150
Ascidiæformes, 508
Ascidians, 505
Ascones, 222, 225
Ascyssa, 224
Asellidæ, 442
Asellus, 440
Asexual reproduction, 140, 143
Asilidæ, 493
Asp, 601
Aspergillum, 368
Aspidobranchia, 378
Aspidonectes, 596
Aspidotus, 490
Ass, 641
Assimilation, organs of, 102
Astacidæ, 435
Astacoidea, 435
Astacus, 431, 432, 435
Astarte, 367
Astartidæ, 368
Asterias, 337
Asterias, early development, 146, 148
Asteridæ, 337
Asterinidæ, 337
Asteriscus, 335, 337, 564
Asteroidea, 333
Astræa, 261
Astrangia, 260, 261
Astroides, 261
Astrophyton, 338
Asymmetrical form, 135

Asymmetron, 504
Atalapha, 638
Atax, 454
Ateles, 651
Atelodus, 641
Atheca, 595
Atlantidæ, 380
Atlas, 581, 590
Atoke, 310
Atoll, 258
Atolla, 250
Atrium, 111, 506, 508
Atrypa, 328
Attus, 453
Atypus, 453
Auchenia, 643
Auditory meatus, 545
Auditory nerve, 536
Auditory organs, 127
Auk, 615
Aulacantha, 196
Aulophorus, 315
Aulosphæra, 196
Aurelia, 245, 250
Auricle, 111, 548
Auricularia, 332
Aurochs, 642
Australian region, 176
Autoflagellata, 200
Autoinfection, 215
Autolytus, 313, 314
Aves, 603
Avicularia, 323
Aviculidæ, 367
Aye-Aye, 649
Axial skeleton, 526
Axiothea, 313
Axis, 590
Axis cylinder, 96
Axolotl, 587
Axons, 94
Azoic era, 180
Azygobranchia, 379

Baboons, 651
von Baer, 17
Bætisca, 479
Badger, 647
Balæna, 646
Balænoptera, 646
Balancers, 491
Balaninus, 485
Balanoglossus, 513
Balantidium, 209, 210
Balanus, 423
Baleen, 645
Bandicoot, 633
Barbs 603
Barbules, 603
Barnacles, 423
Basalia, 330, 340, 527
Bascanion, 601
Basioccipital bone, 522
Basiopodite, 410
Basisphenoid bone, 522
Bass, black, 577
Bassomatophora, 383
Bath sponges, 227
Bats, 637
Bdellodrilus, 315
Bdellostoma, 557
Bdelloura, 271
Bears, 647
Beaver, 639
Bedbug, 489
Bee, larva of, 105
Bees, 487
Beetles, 483
Bela, 380
Belemnites, 388
Bellovacensis, 9
Bell's law, 536
Belosepia, 388
Belostoma, 489
Belostomidæ, 489
Beroe, 264
Beroidæ, 264
Bestiarius, 9
Bicidium, 259
Bicoseca, 201
Bicuspid teeth, 626
Big horn, 642
Bilateral symmetry, 131
Bilharzia, 277
Bimana, 650
Biogenesis, fundamental law of, 34

Biology, 4, 57
Bipalium, 271
Bipinnaria, 332
Biradial symmetry, 136
Bird lice, 479
Birds, 603
Birds of paradise, 50, 616
Birgus, 432, 436
Bison, 642
Bittacus, 483
Bivium, 334
Black bass, 577
Black fish, 646
Black flies, 493
Black snake, 601
Bladder, urinary, 552
Bladder worm, 278, 284
Blarina, 637
Blastoderm, 153
Blastodermic vesicle, 155
Blastoidea, 342
Blastomeres, 151
Blastopore, 156
Blastostyle, 242
Blastula, 151, 155
Blatta, 480
Blattidæ, 480
Blind fish, 576
Blissus, 489
Blister beetle, 484
Blood, 88, 111
Blood corpuscles, 88
Blood vessels, 110, 111
Blow flies, 493
Blue birds, 616
Boa, 601
Bobolink, 616
Body cavity, 109
Bojanus, organ of, 363
Bolina, 264
Bombycina, 495
Bombyx, 495
Bonasa, 614
Bone, 86
Bonellia, 317, 318
Book lice, 479
Bopyridæ, 442
Bopyrus, 442
Bos, 642
Bosmina, 417
Botall's duct, 550
Bot flies, 493
Bothriocephalidæ, 287
Bothriocephalus, 281, 283, 287
Bothrops, 601
Botryllus, 510
Bougainvillea, 144, 241
Bovidæ, 642
Bow fin, 574
Box turtle, 596
Brachialia, 340
Brachiolaria, 332
Brachiopoda, 325
Brachycera, 493
Brachyura, 437
Braconidæ, 486
Bradypus, 636
Brain coral, 261
Branchial arch, 524
Branchial chamber, 352, 506
Branchial clefts, 501
Branchial heart, 391
Branchial tree, 348
Branchiata, 408
Branchiomerism, 523
Branchiopoda, 416
Branchiostegal membrame, 56
Branchiostegal rays, 562
Branchiostegite, 431
Branchipidæ, 416
Branchipus, 416
Branchiura, 422
Braula, 493
Breast bone, 518
Brevilinguia, 599
Brissus, 346
Bristles, 311
Bristles, tactile, 126
Bristle tails, 477
Brittle stars, 337
Bronchiole, 548
Bronchus, 547
Bryozoa, 321
Bubalus, 642
Bubo, 617
Buccal cavity, 106

Buccal ganglion, 390
Buccinidæ, 380
Buccinum, 379
Bucerontidæ, 616
Budding, 141
Budding and germ layers, 159
Buffalo, 642
Buffalo leaf hopper, 490
Buffon, 21
Bufo, 588
Bufonidæ, 588
Bugs, 489
Bugula, 324
Bulbus arteriosus, 568
Bulbus olfactorius, 534
Bulimus, 383
Bulla, 381
Bulla ossea, 621
Bunodes, 259
Bunodontia, 641
Bunodont teeth, 626
Burbot, 578
Bursa, 331, 338
Bursa copulatrix, 471
Bustard, 615
Buteo, 617
Buthus, 448
Butrinus, 575
Butterflies, 494, 495
Butterflies, leaf, 47
Buzzard, 617
Byssus, 363

Cabbage worm, 496
Cacatua, 616
Cacospongia, 227
Caddis flies, 483
Cæcidotea, 442
Cæcilia, 587
Cæcum, 106, 461, 627
Cænolestes, 633
Cænosarc, 231
Calamoichthys, 573
Calandra, 485
Calanidæ, 421
Calappa, 437
Calcispongiæ, 225
Caligidæ, 422
Caligus, 422
Callianira, 263
Calliphora, 493
Callorhinus, 648
Calosoma, 484
Calycella, 242
Calyconectæ, 244
Calycophoræ, 244
Calycozoa, 250
Calyptoblastea, 242
Camarasaurus, 596
Cambarus, 435
Cambrian, 180
Camelopardalidæ, 642
Camels, 643
Camelus, 643
Campanella, 242
Campanula Halleri, 564
Campanularia, 232, 233
Campanulariæ, 239, 242
Camper's angle, 624
Campodea, 400, 477
Canal, radial, 331
Canal, ring, 331
Canal, semi-circular, 128
Canals of sponges, 223
Cancer, 437
Cancridæ, 437
Candona, 423
Canidæ, 647
Canine teeth, 625
Canis, 647
Canker worms, 494
Cannostomæ, 250
Cantharidæ, 484
Canthocamptus, 421
Capillaries, 111
Capillitium, 199
Capra, 642
Caprella, 440
Caprimulgidæ, 616
Capsule, central, 193
Capybara, 639
Carabidæ, 484
Carapace, 410, 594
Carboniferous, 180
Carcharinus, 571
Carcharodon, 571

Carchesium, 210, 211
Cardiidæ, 367
Cardinal teeth, 359
Cardinal vein, 549
Cardium, 367
Cardo, 463
Caridea, 434
Carina, 424
Carina sterni, 605
Carinaria, 380
Carinariidæ, 380
Carinella, 291
Carinatæ, 613
Carnassial teeth, 626
Carnivora, 646
Carotid artery, 549
Carp, 576
Carpal bones, 529
Carpocapsa, 494
Cartilage, 86
Cartilage bone, 519
Cartilaginous cranium, 519, 520
Caryogamy, 184
Caryophyllæus, 285, 286
Caryophyllæidæ, 285
Caryophyllia, 257, 260
Cassowary, 613
Castor, 639
Castoridæ, 639
Casuarina, 613
Casuarius, 613
Cataclysm theory, 20
Catallacta, 220
Catarrhinæ, 651
Caterpillars, 494, 495
Catfish, 576
Cathartes, 617
Cathartidæ, 616
Catocala, 495
Catometopa, 437
Catostomidæ, 576
Cats, 647
Cattle, 642
Caudal fin, 526, 562
Caudina, 347, 349
Causal foundation of theory of evolution, 43
Cavia, 639
Caviare, 573
Cavicornia, 642
Caviidæ, 639
Cavolinidæ, 382
Cebidæ, 651
Cebus, 651
Cecidomyia, 492
Cell, 58
Cell complexes, 71
Cell division, 68
Cell, nature of, 60
Cell organs, 183
Cell-reticulum, 61
Cell theory, 17, 58
Cells, adhesive, 264
Cells, blood, 88
Cells, contractile fibre, 92
Cells, division of, 68
Cell, egg, 80
Cells, ganglion, 94
Cells, gland, 76
Cells, goblet, 77
Cells, muscle, 92
Cells, multiplication of, 68
Cells, nettle, 229
Cells, sexual, 143
Cells, somatic, 143
Cells, supporting, 83
Cells, thread, 229
Cells, yellow, 195
Cellular connective tissue, 84
Cellularia, 324
Cellulose, 172, 505
Cenozoic era, 181
Centipedes, 459, 461
Central capsule, 193
Central nervous system, 122
Centrifugal nerve tracts, 94
Centripetal nerve tracts, 94
Centrodorsal, 338
Centrolecithal eggs, 152, 153
Centrosome, 190
Centrum, 518
Centrurus, 448
Cephalaspis, 557
Cephalochordia, 502
Cephalodiscus, 514
Cephalopoda, 384

Cephalothorax, 399
Cephalothrix, 291
Cerambycidæ, 485
Ceraospongiæ, 227
Ceratium, 203
Ceratodus, 579
Ceratorhinus, 641
Cercaria, 268, 276
Cercomonas, 202
Cercopidæ, 489
Cercus, 477
Cere, 604
Cerebellar hemispheres, 535
Cerebellum, 535
Cerebral flexures, 624
Cerebral ganglion, 123
Cerebral hemispheres, 534
Cerebratulus, 292
Cerebrum, 534
Ceresa, 490
Cereus, 253
Cerianthus, 255
Cervicornia, 642
Cervidæ, 642
Cervus, 642
Ceryle, 616
Cestidæ, 264
Cestoda, 278
Cestum, 264
Cetacea, 645
Cetochilus, 421
Chælura, 439
Chætæ, 311
Chætiferi, 317
Chætoderma, 358
Chætognathi, 296
Chætonotus, 295
Chætopoda, 306
Chætura, 616
Chain salps, 512
Chalcis, 486
Chalcididæ, 486
Chalina, 227
Chameleon, 599
Chamois, 642
Charadriformes, 615
Charadrius, 615
Charybdea, 250
Chelicera, 445
Chelifer, 450
Chelone, 596
Chelonia, 594
Chelonidæ, 596
Chelydra, 596
Chelydridæ, 596
Chermes, 450
Chevron bones, 518
Chevrotain, 642
Chiastoneury, 373
Chigoe, 494
Chilognatha, 496
Chilomonas, 201
Chilomycterus, 578
Chilopoda, 459, 460
Chilostomata, 324
Chimæra, 572
Chimney swallow, 616
Chimpanzee, 651
Chinch bug, 489
Chiromys, 649
Chiroptera, 637
Chirotes, 599
Chitin, 398
Chiton, 357
Chitonidæ, 356
Chlamydosaurus, 599
Chlamydoselachus, 570
Chloragogue cells, 116
Choanoflagellata, 202
Cholœpus, 636
Chondrilla, 224
Chondrin, 86
Chondrioderma, 199
Chondrocranium, 520
Chondropterygii, 569
Chondrostei, 573
Chone, 313
Chorda dorsalis, 501
Chordata, 501
Chordodes, 304
Chordotonal sense organs, 406
Chorion, 148, 634
Choroid, 540
Choroidea, 131
Choroid coat, 130, 131
Choroid gland, 564

Chromatin, 65
Chromatophores, 387
Chromomonadina, 202
Chrysalis, 494
Chrysomelidæ, 485
Chrysomitra, 244
Chrysopa, 483
Chyle, 550
Chyle vessels, 114
Cicada, 488, 489, 490
Cicadidæ, 489
Cicindelidæ, 484
Ciconia, 615
Ciconiformes, 615
Cidaridea, 345
Ciliata, 204
Ciliated epithelium, 75
Cilioflagellata, 203
Cimbex, 486.
Cinclides, 253
Ciona, 507
Circulatory apparatus, 109
Circulatory organs of vertebrates, 548
Cirolana, 442
Cirri, 312
Cirripedia, 423
Cirrus, 120, 272, 308
Cirrus pouch, 272
Cistenides, 314
Cistudo, 596
Citigrada, 453
Cladocera, 417
Cladocora, 260, 261
Cladoselache, 572
Clamatores, 616
Clams, 368
Class, 10
Classification, difficulties in, 30
Clathrulina, 191, 192
Clava, 241
Clavellinidæ, 510
Clavicle, 528
Claws, 618
Clear wings, 495
Cleavage cavity, 155
Cleavage planes, 151
Cleavage of eggs, 149, 151
Cleavage process, 151
Cleavage, types of, 153
Cleon, 479
Clepsidrina, 213, 215
Clepsinidæ, 321
Clibanarius, 436
Clidastes, 600
Climbing birds, 616
Clione, 382
Clisiocampa, 495
Clitellio, 315
Clitellum, 315
Cloaca, 106, 223, 506, 546
Clothes moth, 494
Clupeidæ, 576
Clymene, 313
Clypeaster, 343, 346
Clypeastroidea, 346
Clypeus, 462
Clytia, 242
Cnemidophorus, 599
Cnidæ, 229
Cnidaria, 228
Cnidocil, 229
Cobra, 601
Coccidæ, 490
Coccidiæ, 215
Coccidium, 215, 216
Coccinellidæ, 485
Coccus, 490
Coccygus, 616
Cochineal, 490
Cochlea, 128, 543
Cockatoos, 616
Cockroach, 480
Cod, 577, 578
Codlin moth, 494
Codosiga, 201, 202
Cœlenterata, 228
Cœlhelminthes, 295
Cœlom, 109, 158
Cœlom of Vertebrates, 545
Cœlomic pouches, 158
Cœlenteron, 228
Cœlodendron, 196
Cœloplana, 264
Cœlopleurus, 343, 345
Cœloria, 260, 261
Cœnurus, 285

Coiter, 13
Cold rigor, 63
Cold-blooded animals, 114
Coleoptera, 483
Collaterals, 94
Collembola, 477
Collozoum, 194
Coloborhombus, 49
Colon, 461
Colony, 164
Coloration, sympathetic, 46
Colossendeis, 456
Colossochelys, 596
Colubriformia, 601
Columba, 614
Columbidæ, 614
Columella, 199, 256, 370, 525, 544, 598
Columns of cord, 533
Colymbidæ, 615
Colymbus, 615
Comatrichia, 199
Comatulidæ, 342
Commissures, 123
Complemental males, 424, 442
Compound eye, 403, 404
Conchiolin, 352
Conch of ear, 545
Condylarthra, 639, 643
Condylura, 637
Cones of eye, 540
Coney, 644
Conidæ, 380
Conjugation, 184, 206
Connective tissues, 83
Conocephalus, 481
Conocladium, 200, 202
Conotrachelus, 485
Contractile fibre cells, 92
Contractile vacuole, 183
Conurus, 616
Conus, 380
Conus arteriosus, 567
Convergent development, 169
Cope, 24
Copelatæ, 506
Copepoda, 417
Copperhead, 601
Copula, 524
Copulation, 147
Coraciformes, 616
Coracoid, 528
Coral, brain, 260, 261
Coral, deer's horn, 261
Coral, organ pipe, 259
Coral, precious, 259
Coral, red, 256
Coral reefs, 258
Coral snake, 601
Corallium, 256, 259
Cordylophora, 239
Coregonus, 576
Corium, 514
Cornea, 130, 131, 541
Cornacuspongia, 227
Coronula, 423, 424
Corpora bigemina, 534
Corpora quadrigemina, 534
Corpus callosum, 623
Corpus striatum, 534
Corpuscles, Miescher's, 218
Corpuscles, Meissner's, 126
Corpuscles, Rainey's, 218
Corpuscles, Vater-Pacinian, 126
Correlation of parts, 14
Corrodentia, 478
Corti, organ of, 543
Corvus, 616
Corvidæ, 616
Corycæidæ, 421
Corydalis, 482
Corymorpha, 241
Costæ, 256
Costal plates, 594
Cotingidæ, 616
Cotton worm, 495
Cottus, 577
Cotyledonary placenta, 634
Coturnix, 614
Cougar, 647
Covering scale, 243
Coverts, 604
Cowries, 380
Coxa, 463
Coxal glands, 445
Crab louse, 491
Crabs, 437

Crab stones, 433
Crangon, 434, 435
Crane flies, 492
Cranes, 615
Crania, 328
Cranial nerves, 536
Craspedon, 235
Craspedota, 235
Crassatella, 359
Crassilinguia, 599
Crayfish, 435
Creodonta, 648
Crepidula, 379
Crepidula, cleavage of egg, 154
Cretaceous, 180
Cribillina, 324
Cribrellum, 452
Crickets, 481
Crinoidea, 338
Crisia, 324
Crista acustica, 127, 542
Crista sterni, 605
Crocodilia, 601
Crocodilus, 602
Crop, 106, 467
Crossbill, 616
Crosses, 27
Crossopterygii, 573
Crotalidæ, 601
Crotalus, 601
Croton bug, 480
Crows, 616
Crura cerebri, 623
Crustacea, 408
Cryptobranchus, 587
Cryptocephala, 313
Cryptochiton, 357
Cryptodira, 596
Cryptoniscus, 442
Cryptopentamera, 484
Crystalline cone, 405
Crystalline style, 364
Ctenidia, 353
Cteniza, 453
Ctenobranchia, 379
Ctenodiscus, 337
Ctenoid scale, 558
Ctenolabrus, 576
Ctenophora, 261
Ctenoplana, 264
Ctenostomata, 324
Cubomedusæ, 250
Cuckoos, 616
Cuculiformes, 616
Cuculus, 616
Cucumaria, 349
Culcita, 334, 337
Culicidæ, 492
Cumacea, 437
Cunina, 242
Cunocantha, 239, 242
Curculio, 485
Currant worm, 494
Cursorial foot, 614
Cursoria, 480
Cuspidaria, 368
Cutaneous artery, 585
Cuticle, 75
Cutis, 514
Cuttle bone, 388, 395
Cuttle fish, 395
Cuvier, 14, 15
Cuvierian ducts, 548, 567
Cuvierian organs, 348
Cyamus, 440
Cyanea, 250
Cyanocitta, 616
Cycladidæ, 368
Cyclas, 368
Cycloid scale, 558
Cyclometopa, 437
Cyclostomata, 324, 555
Cyclostomidæ, 380
Cyclopidæ, 421
Cyclops, 37, 421
Cydippidæ, 264
Cygnus, 615
Cymbulidæ, 382
Cymothoa, 440, 442
Cynipidæ, 486
Cynocephalus, 651
Cynomorphæ, 651
Cynomys, 639
Cynthia, 510
Cynthiidæ, 510
Cypræidæ, 380

Cyprididæ, 423
Cypridina, 423
Cypridinidæ, 423
Cyprinidæ, 576
Cypris, 423
Cypselidæ, 616
Cypselomorphæ, 616
Cyrtidæ, 196
Cyrtophilus, 481
Cysticercoid, 285
Cysticercus, 278, 284
Cystid, 322
Cystidea, 342
Cystoflagellata, 203
Cystonectæ, 244
Cytoblast, 58
Cytopharynx, 183
Cytopyge, 183
Cytosporidæ, 213
Cytostome, 183

Dactylethra, 588
Daddy long-legs, 450
Daphnia, 417, 418
Daphnidæ, 417
Dart sac, 376
Darwin, 23
Darwinian theory, 25
Dasyatis, 572
Dasypodidæ, 636
Dasypus, 636
Dasyuridæ, 633
Dasyurus, 633
Datames, 450
Decapoda, 394, 429
Deer, 642
Degeneration, 167
Delamination, 157
Delphinus, 646
Demibranch, 566
Demodex, 454
Dendrites, 94
Dendrocœlum, 271
Dendrœca, 616
Dendronotus, 382
Dental formula, 626
Dentalium, 369
Dentary bone, 525, 582
Denticetæ, 645, 646
Dentine, 515
Derma, 514
Dermal teeth, 515
Dermanyssus, 454
Dermatobia, 493
Dermatoptera, 480
Dermochelys, 595
Dero, 315
Derotrema, 587
Desmodont hinge, 359
Desmodus, 638
Desor's larva, 291
Deutocerebrum, 462, 468
Deutomerite, 214
Deutoplasm, 80
Devexa, 642
Devonian, 180
Diaphragm, 546
Diapophysis, 518
Diaptomus, 421
Diastema, 638
Diastictis, 494
Diapheromera, 480
Diastylis, 437
Dibranchia, 394
Dicotyle, 641
Dicyemida, 220
Didelphia, 632
Didelphys, 633
Didus, 614
Differentiation of tissues, 71
Difflugia, 198
Diffuse nervous system, 122
Diffuse placenta, 634
Digger wasps, 486
Digenea, 274
Digestive tract, 103
Digitigrade, 647
Dimorphodon, 602
Dimyaria, 367
Dinichthys, 579
Dinobryon, 200, 202
Diomedia, 615
Dinoflagellata, 203
Dinoceras, 643
Dinornithidæ, 613
Dinosauria, 596

Dinotheridæ, 644
Dinotherium, 644
Diœcious, 118
Diopatra, 313
Diotocardia, 378
Diphasia, 242
Diphycercal fin, 41, 562
Diphyes, 244, 245
Diphyodont, 625
Diploblastica, 230
Diplocardia, 316
Diplopoda, 459, 496
Diploria, 261
Diplospondyli, 570
Diplozoon, 273
Diplozoon, development of, 165
Dipneumones, 453
Dipneumonia, 579
Dipneusti, 579
Dipnoi, 579
Diporpa, 165, 274
Diprotodon, 634
Diprotodonta, 633
Diptera, 491
Dipurena, 240, 242
Dipylidium, 287, 289
Direct development, 160
Directive corpuscles, 140
Directive spindle, 146
Directives, 254
Discina, 328
Discodermia, 226
Discodrilidæ, 315
Discoidal placenta, 634
Discomedusæ, 250
Disconanthe, 245
Discophori, 318
Dispermy, 148
Distaplia, 510
Distichalia, 340
Distichopus, 315
Distomiæ, 274
Distomum, 116, 272, 275, 276
Distribution, 40
Disuse, 55
Division of labor, 72, 165
Dobsons, 482
Docoglossa, 378
Docophorus, 479
Dodo, 614
Dog-day harvest fly, 489
Dogfish, 569, 571
Dog, prairie, 639
Dog sharks, 571
Dogs, 647
Dolichonyx, 616
Doliolum, 512
Dolomedes, 453
Dolphins, 646
Dondersia, 358
Doridiidæ, 382
Doris, 382
Doryphora, 485
Dorsal aorta, 548
Dorsal fin, 526, 562
Dorsal organ, 341
Draco, 599
Dragon flies, 479
Dranculus, 303
Dreissenia, 367
Drepanidotænia, 289
Drills, 651
Dromæus, 613
Dromatherium, 632
Drum of ear, 544
Duck, 615
Duckbill, 632
Ducts, genital, 120
Ductus Botallii, 550
Ductus choledochus, 546
Ductus cochlearis, 543
Ductus ejaculatorius, 120
Dugong, 645
Duplicidentata, 639
Dynastes, 484
Dysmorphosa, 241
Dysodont hinge, 359
Dytiscidæ, 484

Eagles, 617
Ear bones, 525
Ear of vertebrates, 542
Earth worms, 315
Ear wig, 480
Ecardines, 328
Ecdysis, 399

Echeneis, 577
Echidna, 631, 632
Echidnidæ, 632
Echinarachnius, 345, 346
Echinobothrium, 286
Echinocardium, 346
Echinococcus, 288
Echinoderidæ, 295
Echinoderma, 329
Echinoidea, 343
Echinorhynchus, 304
Echinosphærites, 342
Echiuroidea, 317
Echiurus, 317
Eciton, 488
Ecology, 4
Ectethmoid bone, 522
Ectochondrostoses, 519
Ectocyst, 322
Ectoderm, 103, 156
Ectoparasites, 169
Ectopistes, 614
Ectoprocta, 322
Ectosarc, 189
Edentata, 635
Edriophthalmata, 438
Edrioasteroidea, 342
Edwardsia, 253, 255, 259
Edwardsiella, 259
Egg cell, 80
Egg of bird, 153
Egg, cleavage of, 149, 151
Egg, fertilization of, 147
Egg, maturation of, 146
Egg nucleus, 146, 149
Egg, segmentation of, 149, 151
Egg tooth, 593
Eichhorn, 13
Eiderduck, 615
Eimeria, 213
Elaps, 601
Elasipoda, 349
Elasmobranchii, 569
Elastic cartilage, 86
Elastic tissue, 85
Elastica externa, 516
Elastica interna, 516
Elastin, 85
Elater, 199
Electric catfish, 576
Electric eel, 576
Electric organs, 563
Elephantiasis, 304
Elephantidæ, 644
Elephants, 643
Elephas, 644
Elytra, 312, 466
Embiotocidæ, 577
Embryo, 160
Embryology, 3, 139, 160
Emu, 613
Enamel, 515
Enchylema, 62
Enchytræidæ, 315
Encyrtidium, 193, 196
Encystment, 184
Endite, 410
Endocyst, 322
Endolymph, 127, 543
Endolymphatic duct, 542
Endopodite, 410
Endostyle, 506
English sparrow, 616
Enhydris, 647
Enopla, 290
Ensatella, 368
Entalis, 369
Entelops, 635
Enterocœle, 109
Enteroponeusta, 512
Entoconcha, 349
Entochondrostoses, 519
Entoderm, 103, 156
Entomobrya, 477
Entomostraca, 414
Entoniscus, 441
Entoniscidæ, 441, 442
Entoparasites, 169
Entophaga, 486
Entoplastron, 594
Entoprocta, 321
Entosarc, 189
Entovalva, 349
Environment, 54
Eocene, 181
Eohippus, 643

Eozoon, 180, 198
Epaxial muscles, 518
Epeira, 451, 453
Ependyma, 124, 532
Ephemera, 479
Ephemerida, 479
Ephippium, 417
Ephydatia, 227
Ephyra, 246, 248, 249
Epiblast, 156
Epibdella, 274
Epididymis, 320, 552
Epigenesis, 16
Epiglottis, 547
Epimerite, 214
Epiotic bone, 522
Epipharynx, 463
Epiphragm, 372
Epiphysis, 535
Epiplastron, 595
Epipleural bones, 574
Epipodite, 410
Epipodium, 369
Epipterygoid bone, 598
Episternum, 528
Epistropheus, 590
Epistylis, 208, 211
Epitheca, 256
Epithelial tissues, 73
Epithelium, germinal, 118
Epitoke, 311
Epizoanthus, 170, 259
Equatorial furrow, 151
Equatorial plate, 69
Equidæ, 641
Equilibration, organs of, 128
Equus, 641, 643
Erax, 493
Erethyzon, 639
Eretmochelys, 596
Erichthus, 429, 430
Erigone, 453
Erinacidæ, 637
Eristalis, 493
Ermine, 647
Errantia, 313
Erythroblasts, 89
Erythroneura, 490
Eschara, 324
Esocidæ, 576
Essence of pearl, 558
Estheria, 417
Estheriidæ, 417
Ethiopian region, 176, 178
Ethmoidalia, 521
Ethmoid bone, 523, 620
Euchilota, 240
Eucopepoda, 421
Eucratea, 324
Eucrinoidea, 342
Eudendrium, 232, 242
Eudoxia, 166, 244
Euflagellata, 202
Euglena, 200, 202
Euglenidæ, 202
Euglypha, 198
Euisopoda, 442
Eumeces, 599
Eunectes, 601
Eunice, 311
Eunicidæ, 313
Eupagurus, 170, 435, 436
Euphausia, 429
Euplectella, 226
Euplexoptera, 480
Eupolia, 292
Euryalidæ, 338
Eurypauropus, 497
Eurypterida, 444
Eurypterus, 444
Euselachii, 571
Euspongia, 221, 227
Eustachian tube, 544
Eustachius, 12
Eusuchia, 602
Eutainia, 601
Eutima, 240
Evadne, 417, 419
Everyx, 495
Evolution, 16
Evolution, Theory of, 19, 25
Evolution vs. Creation, 22
Excreta, 73, 103
Excretory organs, 115
Excretory organs of Vertebrates, 550
Exite, 410

Exoccipital bone, 522
Exocœtidæ, 576
Exocœtus, 576
Exopodite, 410
Eugyra, 510
Extracapsulum, 193
Exumbrella, 235
Eyes, 129
Eyes of Vertebrates, 539
Eye spot, 183

Fabricius, 13
Face, bones of, 525
Faceted eye, 403, 404
Facial nerve, 536
Factors of evolution, 44
Fairy shrimp, 417
Falciform spores, 215
Falco, 617
Falcons, 617
Falconiformes, 616
Fasciolaria, 276
Fat body, 407, 468
Faunal provinces, 175
Favia, 260, 261
Favositidæ, 259
Feather tracts, 603
Feathers, 603
Feathers, molting of, 611
Fecundation, 147
Felidæ, 647
Felis, 647
Femoral pores, 589
Femur, 463, 529
Fenestra ovalis, 544
Fenestra rotunda, 544, 593
Fertility of hybrids, 29
Fertilization of eggs, 147, 148
Fertilization in Protozoa, 206
Fibre, 639
Fibres, nerve, 94
Fibula, 529
Fibulare, 529
Fiddler crab, 437
Field mice, 639
Fierasfer, 349
Filaments, mesenterial, 252
Filar substance, 61
Filaria, 303
Filibranch, 362
Filibranchiata, 365
Fin backs, 646
Finches, 616
Fins, 526, 562
Fireflies, 484
Firmisternia, 588
Fish hawk, 617
Fishes, 557
Fishes, tails of, 41
Fishes, circulation in, 112
Fissilinguia, 599
Fissipedia, 647
Fissurella, 378
Fissurellidæ, 379
Fissures of the cord, 532
Flabellum, 410
Flagellata, 200
Flagellate epithelium, 75
Flagellum, 376
Flame cell, 116, 280
Flamingo, 615
Flat worms, 267
Flea, snow, 477
Fleas, 493
Flesh flies, 493
Flies, 491
Flies, black, 493
Flies, blow, 493
Flies, bot, 493
Flies, caddis, 483
Flies, crane, 492
Flies, dragon, 479
Flies, fire, 484
Flies, flesh, 493
Flies, gall, 486
Flies, harvest, 489
Flies, Hessian, 492
Flies, horse, 493
Flies, house, 492, 493
Flies, May, 479
Flies, robber, 493
Flies, saw, 485, 486
Flies, Spanish, 484
Flies, stone, 479
Fluke, 276
Flustra, 324

Flustrella, 324
Flying fish, 576
Flying foxes, 638
Flying squirrel, 639
Fodientia, 636
Fontanelles, 521
Food vacuole, 183
Food yolk, 80
Foot, 351
Foramen magnum, 522
Foramen Panizzæ, 592
Foraminifera, 196
Fore brain, 533
Fore gut, 104
Forficula, 480
Formative yolk, 80
Formicariæ, 487
Fossa rhomboidalis, 535
Fossores, 486
Fowl, 613
Fowl, digestive tract of, 105
Fowl, egg of, 153
Foxes, 647
Frenulum 494
Fringillidæ, 616
Fritillaria, 506
Frogs, 588
Frons, 462
Frontal bone, 523
Frontal sinus, 624
Frontoparietal bone, 581
Frugivora, 638
Fulcra, 573
Function, change of, 100
Function, community of, 165
Fungia, 261
Fungiacea, 261
Funiculus, 322
Furca, 420
Furcula, 605
Fur seal, 648

Gadidæ, 578
Gadus, 577, 578
Galea, 463
Galeidæ, 571
Galen, 12
Galeodes, 450
Galeopithecidæ, 649
Galeopithecus, 637, 649
Galeus, 571
Gall flies, 486
Gallinacea, 613
Galls, 486
Gallus, 614
Gamasidæ, 454
Gamasus, 400, 454
Gammarina, 439
Gammarus, 439
Ganglion, buccal, 390
Ganglion cells, 94
Ganglion, cerebral, 123
Ganglion, optic, 129
Ganglion, stellate, 390
Ganglion, supraœsophageal, 123
Ganglionic nervous system, 122
Ganoid scale, 572
Ganoidei, 558
Ganoin, 558
Gapes, 302
Garpike, 574
Garter snake, 601
Gasteropoda, 369
Gasterosteus, 577
Gastral tentacles, 246
Gastrochæna, 368
Gastrophilus, 493
Gastrotricha, 295
Gastrovascular space, 228
Gastrovascular system, 109
Gastrula, 156
Gastrulation, 156
Gavialis, 602
Gazella, 642
Gecarcinus, 437
Gecko, 598
Gegenbaur, 18
Gelasimus, 437
Gemmaria, 241
Gemmellaria, 324
Gemmulæ, 227
Gemmularia, 241
Gena, 414, 462
Generation, asexual, 140
Generation by parents, 140
Generation, sexual, 142

Generation, spontaneous, 139
Generations, alternation of, 144
Genital ducts, 120
Genital plates, 344
Genus, 10
Geocores, 489
Geodia, 227
Geographical distribution, 174
Geological distribution, 180
Geometrina, 494
Geonemertes, 291
Geophilidæ, 461
Geophilus, 461
Gephyræa, 316
Gerardia, 259
Germinal disc, 152
Germinal epithelium, 118
Germinal vesicle, 81, 146
Germ layer theory, 17
Germ layers and budding, 159
Germ layers, formation of, 156
Geryonia, 242
Geryonid, delamination in, 157
Geryonid, germ layers, 157
Giant cells, 71
Gibbons, 651
Gigantostraca, 443
Gila monster, 599
Gill arch, 524
Gill arteries, 504, 548
Gill clefts, 501, 547
Gill leaves, 361
Gill slits, 501, 547
Gill, tracheal, 469
Gills, 108
Gills of fishes, 565
Gills of vertebrates, 547
Gipsy moth, 119, 495
Giraffa, 642
Girdles, 527
Gizzard, 106, 461
Glabella, 414
Gland cells, 76
Glands, 77
Glands, castor, 618
Gland, choroid, 564
Glands, germinal, 118
Gland, Harder's, 542
Glands, hoof, 618
Gland, lachrymal, 542
Glands, lymph, 550
Gland, lymphoid, 331
Glands, mammary, 619
Glands. milk, 619
Glands, musk, 618
Gland, nidamental, 392
Gland, ovoid, 331
Gland, paraxon, 331
Gland, parotid, 584
Glands, sexual, 80, 117
Glands, sweat, 618
Gland, subneural, 509
Glands, suborbital, 618
Gland, thymus, 547
Gland, thyroid, 547
Glandular epithelium, 73, 76
Glaser's fissure, 621
Glass crab, 436
Glass snake, 599
von Gleichen, 13
Globiceps, 241
Globigerina, 197, 198
Globiocephalus, 646
Glochidium, 364
Glomeridæ, 497
Glomerulus, 117, 552
Glossæ, 464
Glossopharyngeal nerve, 536
Glottis, 547
Glugea, 218
Glutin, 85
Glutton, 647
Glyptodontidæ, 636
Gnathobdellidæ, 321
Gnathochilarium, 496
Goat, 642
Goblet cells, 77
Goblet organs, 307
Goethe, 14, 21
Gœze, 13
Gomphus, 479
Gonads, 117
Goniatites, 394
Goniodes, 479
Gonochorism, 118
Gonodactylus, 429

Gonophore, 238
Gonotheca, 242
Gonys, 604
Goose barnacle, 425
Gopher turtle, 596
Gordiacea, 304
Gordius, 304
Gorgonidæ, 259
Gorilla, 651
Gradientia, 587
Grallatores, 615
Grantia, 225
Grasshoppers, 48, 481
Gray matter, 124, 532
Grebes, 615
Green gland, 411
Green turtle, 596
Gregarina, 213, 215
Gressoria, 480
Gribble, 442
Gromia, 62, 198
Ground substance, 62
Grouse, 614
Gruiformes, 615
Grus, 615
Gryllidæ, 481
Gryllotalpa, 481
Gryllus, 481
Guanin, 558
Guard, 389
Guinea pig, 639
Guinea worm, 303
Gula, 462
Gulls, 615
Gulo, 647
Gunda, 271
Gymnoblastea, 241
Gymnodonti, 578
Gymnolæmata, 323
Gymnonoti, 576
Gymnophiona, 587
Gymnosomata, 382
Gynæcophoral canal, 119
Gynandromorphism, 277
Gyri, 535
Gyrodactylus, 273, 274

Habrocentrum, 453
Haddock, 578
Hadenœcus, 481
Haeckel, 18, 24
Hæmadipsa, 321
Hæmal arch, 516
Hæmal ribs, 518
Hæmal spine, 517
Hæmapophysis, 517
Hæmocœle, 109, 113
Hæmoglobin, 89
Hæmosporida, 216
Hæmuntaria, 321
Hagfishes, 555
Hair, 617
Hair necks, 302
Hair worm, 304
Hairs, auditory, 127
Hairs, tactile, 126
Halcampa, 259
Haleremita, 241
Haliætus, 617
Halibut, 578
Halicore, 645
Halicryptus, 317
Haliomma, 135
Haliommidæ, 196
Haliotidæ, 379
Haliotes, 379
Halisarca, 226
Halitherium, 645
von Haller, 17
Halowises, 239
Halteres, 491
Halyclystus, 250
Hammerhead shark, 571
Hapale, 651
Hapalidæ, 651
Harder's gland, 542
Hares, 639
Harpactidæ, 421
Hatteria, 596
Haustellum, 465
Haversian canals, 87
Haversian lamellæ, 87
Hawks, 617
Head kidney, 310, 550
Head, segments of, 536
Hearing, organs of, 127

Heart, 111
Heart shells, 367
Heat rigor, 63
Hectocotylus, 393
Hedgehogs, 637
Heliaster, 337
Helicidæ, 383
Helioporæ, 259
Heliozoa, 190
Helix, 383
Hell-bender, 587
Hellgrammite, 482
Helminthes, 169
Helminthophaga, 616
Heloderma, 599
Helodermatidæ, 599
Hemelytra, 489
Hemerobiidæ, 482
Hemibranchii, 575, 577
Hemichordia, 512
Hemimetabolous, 473
Hemiptera, 489
Hemitripterus, 577
Hen, 613
Hen clam, 368
Hepatopancreas, 106, 411
Hepatus, 437
Heptanchus, 570
Heredity, 67, 150
Hermaphroditism, 118
Hermit crabs, 436
Herons, 615
Herring, 576
Hesperornis, 612
Hessian fly, 492
Heterakis, 301
Heteraxial symmetry, 136
Heterocercal tail, 41, 562
Heteroconchiæ, 367
Heterocotylea, 273
Heterodera, 300
Heterodont dentition, 625
Heterodont hinge, 359
Heterogony, 144, 145, 486
Heteromera, 484
Heteromyaria, 367
Heteronemertini, 292
Heteronereis, 311
Heteronomy, 138
Heteropleuron, 504
Heteropoda, 380
Heteroptera, 489
Heterosyllis, 311
Heterotricha, 209
Hexacoralla, 259
Hexactinellidæ, 226
Hexamita, 201
Hexanchus, 570
Hexapoda, 461
Hind brain, 533
Hind gut, 104
Hinge, 358
Hinny, 641
Hipparion, 643
Hippasterias, 337
Hippidæ, 437
Hippocampus, 578
Hippocrates, 12
Hippocrene, 241
Hippoglossus, 578
Hippolyte, 434
Hippopotamidæ, 641
Hippopotamus, 641
Hippospongia, 227
Hirudinei, 318
Hirudo, 321
Hirundinidæ, 616
Hirundo, 616
Holoblastic cleavage, 153
Holoblastic eggs, 152, 153
Holocephali, 572
Holocystites, 342
Holometabolous, 473
Holostei, 573
Holostomate, 371
Holothuria, 349
Holothuria, gastrula of, 158
Holothuridea, 346
Holotricha, 209
Homarus, 435
Homaxial animals, 135
Homo, 651
Homocercal tail, 41, 563
Homoiothermous, 115
Homology, 14, 100
Homonomy, 138

Homoptera, 489
Honey ant, 488
Honeycomb, 641
Hoofs, 618
Hooker, 24
Hoploceras, 643
Hoplorhynchus, 213
Hop worm, 495
Hormea, 324
Hormiphora, 262, 264
Horn bills, 616
Horns of cord, 533
Horned toad, 599
Horn tails, 486
Horse flies, 493
Horse mackerel, 577
Horses, 641
Horseshoe crab, 444
House fly, 492, 493
Human embryo, 35
Humerus, 529
Humming birds, 616
Huxley, 18, 24
Hyæna, 647
Hyænidæ, 647
Hyalea, 381
Hyaleidæ, 382
Hyaline cartilage, 86
Hyalonema, 226
Hyalopus, 198
Hyalospongia, 226
Hyas, 437
Hyatt, 24
Hybrids, 28
Hydnophyton, 488
Hydra, 230, 240
Hydra, section of, 141
Hydrachna, 454
Hydrachnidæ, 454
Hydractinia, 241
Hydranth, 231
Hydraria, 239, 240
Hydrichthys, 240, 242
Hydrobatidæ, 489
Hydrocaulus, 231
Hydrochœrus, 639
Hydrocorallina, 239, 241
Hydrocores, 489
Hydroides, 313
Hydromedusæ, 230
Hydrophilidæ, 484
Hydropolyp, 230
Hydropsyche, 483
Hydrorhiza, 231
Hydrosauria, 594
Hydrotheca, 233
Hydrozoa, 230
Hyla, 588
Hylesinus, 485
Hylidæ, 588
Hylobates, 651
Hylodes, 586
Hymenolepis, 287, 288
Hymenoptera, 485
Hyocrinus, 340
Hyoid arch, 524
Hyoid bone, 524
Hyoid cartilage, 524
Hyomandibular, 524, 525
Hypæna, 495
Hypaxial muscles, 518
Hyperia, 439
Hyperina, 439
Hyperoartia, 557
Hyperotretia, 557
Hypoblast, 156
Hypobranchial groove, 503
Hypoderma, 493
Hypodermis, 398
Hypogeophis, 587
Hypoglossal nerve, 536
Hypopharynx, 463
Hypophysis, 535
Hypoplastron, 595
Hyporachis, 603
Hypotricha, 211
Hyracoidea, 644
Hyracotherium, 643
Hyrax, 644
Hystricidæ, 639
Hystricomorpha, 639
Hystrix, 639

Iapyx, 477
Ibis, 615
Ichneumonidæ, 486

Ichthydium, 295
Ichthyobdella, 321
Ichthyodolurites, 570
Ichthyophis, 585, 587
Ichthyopsida, 555
Ichthyosauria, 594
Ichthyotomi, 572
Icteridæ, 616
Icterus, 616
Idiothermous, 115
Idotea, 441, 442
Idoteidæ, 442
Idyia, 264
Iguanidæ, 599
Ilium, 528
Ilyanassa, 379
Imaginal discs, 476
Impennes, 615
Impregnation, 147
Inbreeding, 29
Incisor teeth, 625
Incus, 525, 544
Indirect cell division, 68
Indirect development, 160
Inermes, 317
Infrabasalia, 340
Infundibulum, 534
Ingluvies, 106, 467
Inia, 645
Inorganic bodies, 133
Inquilines, 486
Insecta, 458
Insectivora, 637
Insects, cleavage of egg, 155
Integripalliata, 367
Interambulacral plate, 335
Intercalaria, 516
Interfilar substance, 62
Interhyal bone, 561
Intermaxillary bone, 525
Intermedium, 529
Interorbital septum, 560
Interparietal bone, 619
Interradius, 246
Intervertebral ligament, 519
Intestine, 106
Invagination, 156
Inversion of retina, 541
Iris, 130, 131
Irritability, 62
Ischial callosities, 651
Ischium, 528
Isinglass, 573
Isis, 259
Isodont hinge, 359
Isopoda, 440
Isoptera, 478
Itch, 454
Iter, 534
Iulidæ, 497
Iulus, 497
Ixodes, 454
Ixodidæ, 454

Jacobson's organ, 539
Jassidæ, 490
Jays, 616
Jigger, 494
Jugal arch, 526
Jugal bone, 526
Jugulares, 562
Jugular vein, 549
June bug, 484
Jurassic, 180

Kallima, 47
Kangaroos, 634
Karyokinesis, 68
Katydid, 481
Keyhole limpets, 379
Kidneys, 116, 550
Kielmeyer, 15
Kinetoskias, 324
King crab, 444
King fishers, 616
Kinosternon, 596
Kiwi, 613
Kœnenia, 449
Kölliker, 18
Kowalewskia, 506
Kowalewsky, 18

Labial cartilage, 534
Labial palpi, 362
Labidura, 480
Labium, 463, 464

Labor, division of, 165
Labridæ, 576
Labrum, 463
Labyrinth, 128, 542
Labyrinthodonta. 586
Lac, 490
Lacerta, 599
Lacertilia, 598
Lacertilidæ, 599
Lace wings, 482
Lachrymal bone, 590
Lachrymal gland, 542
Lacinia, 473
Lacteal dentition, 625
Lacuna, 379
Lacunar blood system, 113
Ladder nervous system, 124
Lady bird, 485
Lady crab, 436
Læmodipoda, 439
Lagena, 543
Lagomys 639
Lama, 643
Lamarck, 14, 22
Lamarckism, 53
Lamblia, 202
Lamellæ, Haversian, 87
Lamellæ bone, 87
Lamellibranchiata, 358
Lamellicornia, 484
Lamellirostres, 615
Lamna, 571
Lamnæ, 618
Lamprey eels, 555, 557
Lampyridæ, 484
Land crab, 437
Lanistes, 372
Lantern of Aristotle, 345
Larus, 615
Larva, 160
Larval organs, 161
Laryngeal cartilages, 524
Lateralia, 424
Lateral line, 537, 564
Lateral teeth, 359
Latrodectes, 451
Laurer's canal, 273
Leaf butterflies, 47
Leaf hoppers, 489
Leatherback tortoise, 595
Leather turtle, 596
Leda, 367
Leeches, 318
Leeuwenhoek, 13
Lemniscus, 304
Lemuridæ, 649
Lemurs, 648, 649
Lens of eye, 130, 131, 541
Lepadidæ, 425
Lepas, 172, 425
Lepidonotus, 313
Lepidoptera, 494
Lepidosauria, 594, 597
Lepidosiren, 579
Lepidosteidæ, 574
Lepidosteus, 574
Lepidurus, 416
Lepisma, 477
Lepralia, 324
Leptalis, 48
Leptasterias, 337
Leptocardii, 502
Leptocephalus, 575
Leptochela, 441, 442
Leptoclinum, 510
Leptodiscus, 204
Leptodora, 417
Leptomedusæ, 239, 242
Leptoplana, 110, 271
Leptostraca, 427
Lepus, 639
Lernæa, 422
Lernæidæ, 422
Lernæocera, 421, 422
Lernæopodidæ, 422
Leucania, 495
Leucetta, 225
Leuckart, 18
Leucocytes, 88
Leucon, 223
Leucones, 226
Leucortis, 226
Leucosoidea, 437
Leucosolenia, 225
Libellula, 479
Libellulidæ, 479

Libinia, 436, 437
Lice, 491
Lice, bird, 479
Lice, book, 479
Life, origin of, 140
Ligula, 286
Ligulidæ. 286
Limacidæ, 383
Limacinidæ, 382
Limax, 383
Limbs of vertebrates, 527
Limicola, 315
Limitans externa, 540
Limitans interna, 540
Limnadia, 417
Limnæa, 383
Limnæidæ, 383
Limnocnida, 239
Limnocodium, 239
Limnoria, 441, 442
Limnothrips, 479
Limpets, 379
Limulus, 444
Linckia, 334
Linear nervous system, 122
Linerges, 250
Lines of growth, 358
Lineus, 289, 292
Lingual ribbon, 355, 373
Linguatulida, 454
Lingula, 328
Linin, 65
Linnæan system, 10
Linnæus, 10
Liobunum, 451
Lion, 647
Liriope, 239, 242
Lithistidæ, 226
Lithobiidæ, 461
Lithobius, 461
Lithodidæ, 437
Lithodomus, 367
Littorina, 379
Littorinidæ, 380
Liver, 106
Liver fluke, 276
Lizards, 598
Lizzia, 240, 242
Lobatæ, 264
Lobate foot, 614, 615
Lobi inferiores, 563
Lobosa, 189
Lobster, 435
Lobster, spiny, 436
Locomotion, 121
Locustidæ, 481
Locusts, 481, 489
Loggerhead, 596
Loligo, 384, 395
Loligo, cleavage of, 155
Longipennes, 615
Loons, 615
Lophobranchii, 578
Lophodont teeth, 626
Lophogastridæ, 429
Lophophore, 324
Lophopoda, 324
Lophopus, 324
Lophs of teeth, 626
Lorica, 200
Loricata, 435, 577, 601, 636
Loris, 649
Lota, 578
Love dart, 376
Loven's larva, 309
Loxia, 616
Loxosoma, 322
Lucernariæ, 250
Luciæ, 510
Lumbricus, 315, 316
Lumbricus, anatomy of, 118
Lunatia, 379, 380
Lung book, 443
Lung fishes, 579
Lungs, 109, 547
Lung sac, 443
Lung sacs of birds, 609
Lutra, 647
Lycosa, 453
Lyell, 23, 24
Lygæidæ, 489
Lymph, 88, 90
Lymph corpuscles, 90
Lymph glands, 550
Lymph system, 550
Lymph vessels, 114

Lymphoid gland, 331
Lyonet, 13
Lyre birds, 616
Lyriform organs, 445
Lytta, 484

Macacus, 651
Macaques, 651
Machilis, 458, 477
Mackerel, 577
Mackerel shark, 571
Macoma, 368
Macræsthete, 357
Macrobdella, 321
Macrobiotus, 455
Macrochelys, 596
Macrochiroptera, 638
Macrodrila, 315
Macrogamete, 185
Macronucleus, 206
Macropodidæ, 633
Macropus, 634
Mactra, 359
Mactridæ, 368
Macrura, 434
Madrepora, 261
Madreporaria, 260
Madreporite, 330
Maioidea, 437
Malaclemmys, 596
Malacobdella, 291
Malacoderma, 259
Malacopoda, 456
Malacopteri, 574
Malacostraca, 426
Malagassy region, 178
Malapterurus, 576
Malar bone, 526, 620
Malaria, 217, 492
Maldanidæ, 313
Malleus, 525, 544
Mallophaga, 479
Malpighi, 13
Malpighian body, 117
Malpighian tubes, 438, 445, 459, 461
Mammalia, 617
Mammals, 617
Mammoth, 644
Man, 651
Manatee, 644
Manatus, 644
Mandible, 401
Mandibles, 463, 464
Mandibular arch, 524
Mandibular cartilage, 524
Mandrils, 651
Manicina, 261
Manis, 636
Manna, 489
Manubrium, 235
Mantidæ, 480
Mantis, 480
Mantis shrimp, 429
Mantle, 351, 505
Mantle cavity, 352
Manyplies, 642
Manyunkia, 313
Margarita, 379
Margelis, 144, 241
Marginal plates, 595
Marine faunæ, 179
Marmosets, 651
Marsipobranchii, 555
Marsupialia, 632
Marsupial bones, 631, 632
Marsupium, 632
Marten, 647
Mastax, 294
Mastigamœba, 188, 201
Mastigophora, 200
Mastodon, 644
Maturation of egg, 146
Maturation and Fertilization, 147
Matuta, 437
Maxilla, 401, 463
Maxillary bone, 525
Maxillary sinus, 624
Maxillipeds, 401
May flies, 479
Measly meat, 284, 285
Measuring worms, 494
Meckel, 14
Meckelia, 292
Mecoptera, 483
Mediastinum, 546
Medulla oblongata, 534

Medullary plate, 501
Medullary sheath, 96
Medusæ, 144, 230, 234
Megalops, 434
Megalonyx, 636
Megalosphæres, 198
Megatherium, 636
Megascolex, 316
Megastoma, 202
Meissner's corpuscles, 126
Melanoplus, 481
Meleagrina, 367
Meleagris, 614
Melitta, 346
Meloidæ, 484
Melolontha, 484
Melonites, 345
Melophagus, 493
Melopsittacus, 616
Membracidæ, 490
Membrane bones, 515
Membranipora, 324
Membranellæ, 209
Membranous cranium, 519
Menopoma, 587
Mentum, 464
Menuridæ, 619
Mephitis, 647
Meridional furrows, 151
Mermithidæ, 304
Meroblastic cleavage, 153
Meroblastic eggs, 152, 154
Meryhippus, 643
Mesectoderm, 222
Mesencephalon, 533
Mesenchyme, 157
Mesenterial filaments, 252
Mesenteries, 109, 545
Mesenteron, 105
Mesethmoid bone, 522
Mesites, 613
Mesoblast, 157
Mesobronchus, 609
Mesoderm, 104, 157
Mesoglœa, 230
Mesohippus, 643
Mesonemertini, 291
Mesonephros, 550
Mesonephric duct, 550
Mesopterygium, 529
Mesorchium, 546
Mesotroche, 309
Mesosternum, 462
Mesothelium, 158
Mesothorax, 462
Mesozoic era, 180
Mesovarium, 546
Metabolism, 172
Metacarpal bones, 529
Metagenesis, 144
Metameres, 137, 305
Metamerism, 137
Metamorphosis, 161
Metamorphosis of insects, 473
Metanemertini, 291
Metanephric duct, 550
Metanephros, 550
Metapodium, 369
Metapterygium, 529
Metastoma, 430
Metatarsal bones, 529
Metathorax, 462
Metazoa, 221
Metencephalon, 533
Methona, 48
Metridium, 259
Miastor, 492
Mice, 639
Micræsthete, 357
Microcentrum, 481
Microchiroptera, 638
Microconodon, 632
Microcotyle, 274
Microdrilæ, 315
Microgametes, 185
Microlepidoptera, 494
Microlestes, 632
Micronucleus, 206
Micropterus, 577
Micropylar apparatus, 148
Microsphæres, 198
Microstomidæ, 271
Microthelyphonida, 448
Micrura, 292
Midas, 651
Mid brain, 533

Middle Ages, Zoology in, 9
Mid gut, 105
Miescher's corpuscles, 218
Migration of birds, 612
Migration theory, 52
Miliola, 197, 198
Milk teeth, 625
Millepora, 233, 241
Mimicry, 46
Mink, 647
Miocene 181
Miohippus, 643
Miracidium, 276
Mites, 453
Mitosis, 68
Mixipterygium, 570
Mnemiopsis, 264
Moccasin, 601
Modiola, 366, 367
Molar teeth, 625
Mole cricket, 481
Moles, 637
Molgula, 510
Molgulidæ, 510
Mollusca, 351
Molpadia, 349
Monactinellidæ, 227
Monadina, 202
Monascidiæ, 510
Monaxial symmetry, 135
Monera, 189
Moniezia, 287, 289
Monitor, 599
Monkeys, 651
Monocaulis, 240, 241
Monocystis, 215
Monodelphia, 634
Monodon, 646
Monogenea, 273
Monogony, 140
Monomyaria, 367
Monops, 271
Monophyodont, 625
Monopneumonia, 579
Monopylea, 196
Monorhina, 556
Monoscelis, 271
Monospermy, 148
Monostomum, 275
Monothalamia, 198
Monotocardia, 379
Monotremata, 631
Moose, 642
Morphology, 2
Morphology, development of, 12
Mosaic vision, 406
Mosasaurus, 600
Moschidæ, 642
Moschus, 642
Mosquitos, 492
Mosquitos and malaria, 217
Moths, 494
Mouse, 639
Mud crab, 437
Mud puppy, 587
Mud turtle, 596
Müller, Fritz, 24
Müller, J., 18
Müller, O. F., 13
Müllerian duct, 551
Müller's fibres, 540
Mule, 641
Multicellular glands, 77
Multicellularity, 70
Multinuclearity, 70
Multituberculata, 632
Muricidæ, 380
Mus, 639
Musca, 492, 493
Muscariæ, 493
Muscidæ, 493
Muscle cells, 92
Muscle fibres, 91
Muscular tissue, 91
Musculature, 121
Musk deer, 642
Musk ox, 642
Musk rat, 639
Mussels, 367
Mustela, 647
Mustelidæ, 647
Mustelus, 571
Mya, 368
Mycetozoa, 198
Myctodera, 587
Myelin, 96

Mygale, 453
Mygalidæ, 453
Mygnimia, 49
Myidæ, 368
Mylodon, 636
Myocommata, 531
Myomerism, 523
Myomorpha, 639
Myopsida, 395
Myosepta, 531
Myotomes, 531
Myrianida, 310, 313
Myriapoda, 408, 459, 496
Myriothelia, 241
Myriotrochus, 349
Myrmecocystus, 488
Myrmecophaga, 636
Myrmecophily, 169
Myrmeleo, 481, 483
Mysididæ, 429
Mysis, 428, 429
Mysticetæ, 645, 646
Mytilus, 363
Myxicolida, 313
Myxidium, 213, 217
Myxine, 557
Myxobolus, 217
Myxomycetes, 198
Myxospongiæ, 225, 227
Myxosporida, 217
Myzobdella, 315
Myzontes, 557

Nacre, 361
Nägeli, 24, 54, 55
Naiadæ, 367
Naididæ, 315
Nails, 618
Nais, 307
Naja, 601
Nandu, 613
Nanomia, 244. 245
Narcomedusæ, 239, 242
Narwal, 646
Nasal bone, 523
Nassa, cleavage of, 154
Nassellaria, 196
Natatores, 614
Naticidæ, 380
Natural selection, 44
Nauplius, 37, 413
Nauplius eye, 412
Nausithoë, 134, 250
Nautilidæ, 394
Nautilus, 387, 394
Nearctic region, 176, 178
Nebalia, 427
Nectonema, 304
Nectonemertes, 291
Necturus, 587
Nectocalyx, 243
Needham's sac, 392
Nematocysts, 229
Nematoda, 298
Nemathelminthes, 298
Nematophora, 228
Nematus, 486
Nemerteans, 289
Nemertini, 289
Nemocera, 492
Nemognatha, 483
Nemopsis, 242
Neocrinoidea, 342
Neogæa, 177
Neomenia, 358
Neotropical region, 176, 177
Nephilis, 321
Nephridia, 116, 308
Nephrostome, 116
Nepidæ, 489
Neptunus, 437
Nereidæ, 313
Nereis, 311, 312, 313
Nerve-end buds, 537
Nerve fibres, 94
Nerve hillock, 537
Nerve roots, 533
Nerves of vertebrates, 535
Nervous system, 122
Nervous tissue, 94
Nettle bodies, 205
Nettle cells, 229
Neural arch, 516
Neural plates, 594
Neural spine. 517
Neurapophysis, 517

Neurenteric canal, 502, 532
Neurites, 94
Neuropodium, 308, 312
Neuropore, 503, 532
Neuroptera, 481
Neverita, 380
New Zealand, 177
Nictitating membrane, 541
Nidamental glands, 392
Night hawks, 616
Nipple, 619
Nirmus, 479
Noctiluca, 201, 203
Noctuina, 495
Nodes of Ranvier, 96
Nomarthra, 636
Nomenclature, binomial, 10
Non-Ruminantia, 641
Nosema, 218
Nothria, 313
Notochord, 501, 515
Notochordal sheath, 516
Notodelphys, 585
Notodelphidæ, 422
Notogæa, 176
Notonectidæ, 489
Notopodium, 308, 312
Nototrema, 585
Notum, 462
Nuclear plate, 595
Nuclear fragmentation, 70
Nuclear spindle, 68
Nuclear substance, 65
Nuclein, 65
Nucleolus, 66
Nucleus, 58, 64
Nucleus, cleavage, 149
Nucleus, egg, 146
Nucleus in fertilization, 149
Nucleus of Salpa, 511
Nucleus, significance of, 67
Nucleus, somatic, 208
Nucleus, sperm, 149
Nucleus, substance of, 65
Nucleus, structure of, 65
Nucula, 365, 367
Nuculidæ, 367
Nuda, 264
Nudibranchia, 382
Nummulites, 198
Nurse, 144
Nutrition and reproduction, 64
Nyctotherus, 210
Nymphon, 456

Obelia, 240, 242
Obisium, 450
Obturator foramen, 622
Occipitalia, 521
Occipital bone, 521, 619
Occiput, 462
Ocellatæ, 239
Ocellus, 129, 403
Ocneria, 119, 495
Octocoralla, 258
Octopoda, 395
Octopodidæ, 395
Octopus, 384, 390, 394, 395
Ocular plate, 335
Oculina, 261
Oculomotor nerve, 536
Odonata, 479
Odontoholcæ, 612
Odontophore, 373
Odontormæ, 612
Odontornithes, 612
Œcanthus, 481
Œcology, 457, 164
Œdipoda, 481
Œdogonium, 173
Œgopsida, 394
Œsophageal ring, 124
Œsophagus, 106, 546
Œstridæ, 493
Œstrus, 193
Oikopleura, 506, 507
Oil bottle, 484
Olfactory organs, 126
Olfactory organs of vertebrates, 538
Olfactory lobe, 534
Olfactory nerve, 536
Oligocene, 181
Oligochætæ, 314
Oligosoma, 599
Oligotrochus, 349
Olividæ, 380

Olynthus, 222
Omasum, 642
Omentum, 546
Ommastrephes, 388, 395
Ommatidium, 405
Oncosphæra, 283
Oniscidæ, 442
Oniscus, 442
Ontogeny, 3, 160
Oospore, 185
Ootype, 272
Opalina, 209
Opercular bones, 562, 566
Opercularella, 242
Operculum, 210, 323, 371, 440, 566
Ophidia, 600
Ophidiaster, 334
Ophiocoma, 338
Ophiocnida, 338
Ophioglypha, 338
Ophiopholis, 338
Ophiothelia, 338
Ophisaurus, 599
Ophisthotic bone, 522
Ophiuroidea, 337
Opisthobranchia, 381
Opisthocœlous, 519
Opisthopatus, 458
Opossums, 633
Opossum shrimp, 428
Opoterodonta, 601
Optic ganglion, 129
Optic lobes, 534
Optic nerve, 536
Optic stalk, 541
Optic thalami, 534
Optic vesicle, 541
Oralia, 330, 340
Orang-utan, 651
Orange scale insect, 490
Orbitelariæ, 453
Obitosphenoid bone, 522
Orchestia, 438, 439
Order, 10
Organic bodies, 133
Organisms, origin of, 139
Organ-pipe coral, 259
Organs, 99
Organs, animal, 101, 121
Organs, of assimilation, 102
Organs, auditory, 127
Organs, of Bojanus, 363
Organs, circulatory, 109
Organs, of Corti, 543
Organs, digestive, 103
Organ, dorsal, 341
Organs, electric, 563
Organs of equilibrium, 128
Organs, excretory, 115
Organs, excretory, of vertebrates, 550
Organ of Jacobson, 539
Organs of hearing, 127
Organs, lateral line, 537
Organs, olfactory, 126
Organs, pearl, 558
Organs, respiratory, 107
Organs, sensory, 125
Organs, sexual, 117
Organs, sexual, of vertebrates, 550
Organs of smell, 126
Organs, systems of, 100
Organs, tactile, 125
Organs, of taste, 126
Organs, of touch, 537
Organs, vegetative, 101, 102
Oriental region, 176, 178
Orioles, 616
Ornithodelphia, 631
Ornithorhynchidæ, 632
Ornithorhynchus, 631, 632
Orohippus, 643
Oronasal groove, 538
Orthis, 328
Orthoceras, 394
Orthonectida, 220
Orthoneurous, 374
Orthopoda, 597
Orthoptera, 480
Orycteropus, 636
Oscarella, 227
Oscines, 616
Osculum, 222, 225
Os en ceinture, 581
Ossein, 86
Os transversum, 590
Os turbinale, 620

Osmerus, 576
Osphradium, 354
Ossicle, auditory, 127
Ostariophysi, 575
Osteoblasts, 88
Ostracoda, 422
Ostracodermi, 557, 578
Ostracoteuthis, 388
Ostræidæ, 367
Ostium tubæ, 552
Ostrich, 613
Otaria, 648
Otic ganglion, 537
Otica, 521
Otis, 615
Otocysts, 236
Otoliths, 127
Otter, 647
Ovibos, 642
Ovicells, 322
Ovidæ, 642
Oviducts, 120
Oviparous, 161
Ovis, 642
Ovoid gland, 331
Ovoviviparous, 161
Owen, 18
Owlet moths, 495
Owls, 617
Ox warble, 493
Oxy-hæmoglobin, 89
Oxyrhyncha, 437
Oxystomata, 437
Oxyuris, 301
Oyster crab, 437
Oysters, 367

Pachydermata, 641
Pachydrilus, 315
Pachylemuridæ, 649
Paddle fish, 573
Pædogenesis, 142, 472
Paguridea, 436
Palæarctic region, 176, 178
Palæmon, 400, 434
Palæmonetes, 434
Palæmonidæ, 434
Palæocrinoidea, 342
Palæotherium, 643
Palæozoic era, 180
Palate, 539
Palatine bone, 525
Paleacrita, 494
Palechinoidea, 345
Paleontology, 4
Paleozoology, 4
Pali, 256
Palinuridæ, 435
Palinurus, 436
Pallial line, 359
Pallial sinus, 360
Pallium, 351, 534
Palmate foot, 614, 615
Palm crab, 436
Palolo, 311
Palpi, labial, 362
Palpus, 430, 463
Paludicella 324
Paludinidæ, 380
Pancreas, 106
Pandalus, 434, 435
Pandion, 617
Pandionidæ, 617
Pangolin, 636
Panopeus, 437
Panorpa, 483
Panorpidæ, 483
Pantopoda, 456
Paper nautilus, 395
Papilio, 496
Parachordals, 520
Paractinopoda, 349
Paradidymis, 552
Paradisea, 50
Paradiseidæ, 616
Paradoxides, 415
Paraglossa, 464
Paragnath, 430
Paramæcium, 206, 207, 209
Paranuclein, 66
Paranucleus, 206
Parapodium, 312, 369
Parapophysis, 518
Parapterium, 604
Paraquadrate bone, 581
Parasita, 422

Parasitism, 167
Parasphenoid bone, 523
Parasuchia, 602
Paraxon gland, 331
Parietal bone, 523
Parietal foramen, 590
Parietal ganglia, 354
Parietal organ, 535
Parostoses, 519
Parotid gland, 584
Parrots, 616
Parthenogenesis, 142, 145, 472
Partial cleavage, 152, 153
Partridge, 614
Parypha, 241
Passer, 616
Passeres, 616
Patagium, 637
Patellidæ, 378
Pathetic nerve, 536
Paunch, 641
Pauropida, 497
Pauropus, 497
Pearl organs, 558
Pearl oysters, 367
Pearls, 361
Pearls, artificial, 558
Pébrine, 218
Peccaries, 641
Pecora, 641
Pecten, 366
Pecten of eye, 611
Pectinatella, 324
Pectines, 447
Pectinibranchia, 379
Pectinidæ, 367
Pectoral fin, 562
Pectoral girdle, 527
Pedal cords, 354
Pedal ganglia, 353
Pedata, 349
Pedes spurii, 475
Pedicellina, 322, 330
Pediculati, 575
Pediculus, 491
Pedipalpi, 448
Pedipalpus, 445
Pelagia, 246, 250
Pelecanus, 615
Pelecypoda, 358
Pelicans, 615
Pelmatozoa, 338
Pelobatidæ, 588
Pelomyxa, 189
Peltogaster, 426
Pelvic fin, 526, 562
Pelvic girdle, 527
Pen, 389
Peneidæ, 434
Penella, 422
Peneus, 434
Penguin, 615
Penis, 120
Pennaria, 241
Pennatula, 259
Pennatulidæ, 259
Pentacrinus, 339, 342
Pentacta, 349
Pentadactyle appendage, 529
Pentamera, 484
Pentamerus, 328
Pentastomum, 169, 445
Pentatomidæ, 489
Pentatoma, 489
Pentremites, 342
Perameles, 633
Peramelidæ, 633
Perca, 574, 577
Perch, 577
Percidæ, 577
Perdix, 614
Pereiopoda, 401
Perforata, 197, 198
Peribranchial chamber, 503, 505
Pericardial sinus, 470
Pericardium, 111, 546
Perichæta, 316
Perichondrium, 86
Pericolpa, 250
Peridinium, 203
Perilymph, 543
Periosteum, 87
Peripatidæ, 456
Peripatopsis, 458
Peripatus, 456, 458
Peripharyngeal band, 506

Peripheral nervous system, 122
Periphylla, 250
Periplaneta, 480
Periproct, 343
Peripylea, 195
Perisarc, 233
Perissodactyla, 640, 641
Peristome, 209, 343
Peritoneal cavity, 546
Peritoneum, 109, 546
Periwinkle, 380
Perla, 479
Perlidæ, 479
Permian, 180
Perennibranchiata, 587
Peromedusæ, 250
Perophora, 510
Peropoda, 601
Perradius, 246
Petaurus, 634
Petiole, 485
Petoscolex, 315
Petromyzon, 557
Petromyzon, cleavage of egg, 154
Petromyzontes, 557
Petrosal bone, 522
Phacellæ, 246
Phænicopterus, 615
Phæodaria, 196
Phæodium, 196
Phaethon, 615
Phagocata, 271
Phalanges, 529
Phalangida, 450
Phalangistidæ, 634
Phalangium, 451
Phallusia, 509
Pharyngeal bones, 560, 576
Pharyngognathi, 576
Pharynx, 106, 506, 546
Phascalosoma, 316, 317
Phascolomyidæ, 633
Phascalomys, 633
Phascolion, 317
Phasianella, 379
Phasianidæ, 614
Phasianus, 614
Phasmidæ, 480
Phasmomantis, 480
Pheasants, 614
Phenacodon, 639
Phenacodontidæ, 643
Phidippus, 453
Philichthys, 38
Philine, 381
Philonexidæ, 395
Phlegethontias, 495
Phoca, 648
Phocidæ, 648
Pholadidæ, 368
Phoronidea, 325
Phoronis, 325
Phoxichilidium, 456
Phragmocone, 389
Phronima, 439
Phryganea, 483
Phrynicus, 448
Phrynoidea, 448
Phrynosoma, 599
Phrynus, 448
Phthirius, 491
Phylactolæmata, 324
Phyllium, 48
Phyllodactylus, 598
Phyllopoda, 415
Phyllosoma, 434, 436
Phyllostomidæ, 638
Phylloxera, 491
Phylogeny, 4, 31
Physalia, 245
Physeter, 646
Physiological character of species, 27
Physiologus, 9
Physiology, 3
Physoclisti, 567
Physonectæ, 244
Physophora, 244
Physophoræ, 244
Physopoda, 479
Physostomi, 567, 575
Phytoflagellata, 202
Phytophaga, 633
Picariæ, 616
Picas, 639
Pickerel, 576
Picus, 616

Pieris, 496
Pieris, cleavage of, 155
Pigeons, 26, 27, 614
Pigmented epithelium, 540
Pike, 576
Pilidium, 290, 291
Pill bug, 442
Pineal eye, 535
Pinealis, 535
Pinnipedia, 647
Pinnotheres, 437
Pinnulæ, 340
Pin worm, 301
Pipa, 585, 588
Pipe fish, 578
Pisces, 557
Piscicola, 321
Pisidium, 368
Pituitary body, 535
Placenta, 634
Placentalia, 634
Placoid scale, 515, 558
Placophora, 356
Plagiaulax, 632
Plagiotremata, 597
Plagiostomi, 569
Planaria, 271
Planarians, 268
Planipennia, 482
Plankton, 179
Planorbis, 383
Plantigrade, 647
Plant lice, 490
Plants and animals, 171
Planula, 237
Plasma, blood, 88
Plasmic products, 64, 72
Plasmodium, 198, 216
Plastin, 66
Plastogamy, 184
Plastron, 594
Platanista, 645
Plathelminthes, 267
Platyonichus, 436, 437
Platyrrhinæ, 651
Plecoptera, 479
Plectognathi, 578
Pleistocene, 181
Pleopoda, 401, 402
Plesiosauria, 594
Plethodon, 587
Pleura, 414, 462, 546
Pleuracanthus, 572
Pleural cavity, 546
Pleural cords, 354
Pleural ribs, 518
Pleurobrachia, 262, 264
Pleurocercoid, 283
Pleurodira, 596
Pleurodont teeth, 599
Pleuronectidæ, 578
Pleuroperitoneal cavity, 546
Plictolophus, 616
Pliocene, 181
Pliohippus, 643
Pliny, 8
Plover, 615
Plumularia, 242
Plumatella, 324
Pluteus, 332
Pneumatic duct, 567
Pneumaticity of bones, 608
Pneumatophore, 243
Pneumodermon, 382
Pneumogastric nerve, 536
Podocoryne, 241
Podophrya, 68, 212
Podophthalmia, 427
Podura, 477
Poikilothermous, 115
Polar bodies, 146
Pole field, 263
Poles of egg, 147, 151
Polian vesicles, 331
Polistotrema, 557
Polybostrichus, 311
Polychætæ, 311
Polychœrus, 269, 271
Polycladidea, 269, 271
Polyclinum, 510
Polyclonia, 247, 251
Polycystidæ, 214
Polydesmidæ, 497
Polyergus, 488
Polygordius, 309, 314
Polymorphism, 165

Polynesia, 177
Polynoe, 313
Polynoidæ, 313
Polyodon, 573
Polyodontidæ, 573
Polyp, 230
Polyphemidæ, 417
Polypid, 322
Polypodium, 239, 241
Polyprododonta, 633
Polypterus, 573
Polypterus tail, 41
Polyscelis, 271
Polyspermy, 148
Polystomeæ, 273
Polystomella, 198
Polystomum, 273, 274
Polythalamia, 196, 198
Polytroche, 309
Polyzoa, 321
Poneridæ, 487
Pons Varolii, 623
Pontobdella, 321
Pontodrilus, 308
Pontella, 421
Porcellanidæ, 437
Porcellain crabs, 437
Porcellio, 442
Porcellio, nervous system of, 124
Porcupines, 639
Porella, 324
Pori abdominales, 546
Porifera, 221
Porites, 261
Porpita, 245
Portal vein, 548
Portuguese man-of-war, 245
Portunidæ, 437
Porus branchialis, 503
Postabdomen, 401
Postfrontal bone, 526, 590
Postorbital bone, 590
Postpermanent dentition, 625
Potato beetle, 485
Powder down, 603
Præclavia, 528, 622
Præcoces, 612
Prairie dogs, 639
Praya, 166, 244
Prefrontal bone, 526, 590
Prelacteal dentition, 625
Premaxillary bone, 525
Premolar teeth, 626
Presphenoid bone, 522
Priapuloidea, 317
Priapulus, 317
Primaries, 604
Primary bone, 519
Primary yolk, 80
Primates, 649
Primnoa, 259
Primordial cranium, 521
Principal tissue, 99
Priodon, 635
Pristidæ, 572
Pristis, 572
Proboscidia, 643
Proboscis, 373
Procœlous, 519
Procoracoid, 528
Proctodæum, 104
Procyon, 647
Prœchidna, 631, 632
Proglottids, 278
Profeet, 466
Progression, principle of, 55
Prolegs, 475
Promorphology, 133
Pronephric duct, 550
Pronephros, 550
Prong horn, 643
Pronotum, 462
Pronucleus, 149
Proofs of phylogeny, 32
Proostracum, 389
Prootic bone, 522
Propodium, 369
Propterygium, 529
Prorostomus, 644
Prosencephalon, 533
Prosimiæ, 648
Prosobranchia, 378
Prosternum, 528
Prostoma, 156
Protamœba, 189
Proteroglypha, 601

Proteroglyphic tooth, 600
Proteus, 587
Prothorax, 462
Protobranchiata, 365
Protista, 186
Protocaris, 416
Protocerebrum, 462, 468
Protoconchiæ, 365
Protodonta, 632
Protohydra, 239, 241
Protomerite, 214
Protonemertini, 291
Protonephridia, 115
Protoplasm, 61, 80
Protoplasm, discovery of, 59
Protoplasm, movement of, 62
Protopterus, 579
Prototheria, 631
Protovertebræ, 531
Protozoa, 183
Prortacheata, 408, 456
Protula, 313
Proventriculus, 467
Psammonyx, 198
Pseudelectric organs, 563
Pseudobranch, 570
Pseudocuticula, 597
Pseudolamellibranchiata, 365
Pseudonavicellæ, 215
Pseudoneuroptera, 477
Pseudopodia, 187
Pseudoscorpii, 450
Pseudosuchia, 602
Psittaci, 616
Psittacus, 616
Psocidæ, 479
Psolus, 349
Psorosperms, 217
Pteranodon, 602
Pteraspis, 557
Pterichthys, 557
Pterodactylia, 602
Pteronarcys, 479
Pteropoda, 382
Pteropod ooze, 382
Pteropus, 638
Pterosauria, 602
Pterotic bone, 522, 560
Pterotracheidæ, 380
Pterygoid bone, 525
Pterygoid process, 622
Pterygoquadrate, 524
Pterygotus, 444
Pterylæ, 603
Pubic bone, 528
Pugettia, 437
Pulex, 493, 494
Pulmonata, 383
Pulmonary artery, 549
Pulmonary circulation, 549
Pulmonary vein, 549
Pulp cavity, 515
Pulvilla, 493
Puma, 647
Pupa, 383
Pupæ, 474
Pupipara, 493
Purpura, 379, 380
Putorius, 647
Pycnogonida, 456
Pygidium, 414
Pyloric cæca, 565
Pylorus, 546
Pyrosoma, 510
Pyrula, 373
Python, 601
Pythonaster, 337
Pythonomorpha, 600

Quadrula, 196, 198
Quadrumana, 650
Quadrate bone, 525
Quahog, 368
Quail, 614
Quaternary, 181

Raccoon, 647
Rachis, 603
Racemose glands, 77
Radial canals, 235, 331
Radial symmetry, 135
Radiale, 529
Radialia, 330, 340, 527
Radiata, 228, 329
Radiolaria, 192
Radius, 529

Radula, 355, 373
Raia, 571, 572
Raiidæ, 572
Rail, 615
Rainey's corpuscles, 218
Rallus, 615
Rana, 588
Ranatra, 489
Rangifer, 642
Ranvier, nodes of, 96
Raptores, 616
Raptorial foot, 614
Rasorial foot, 614
Rasor clam, 368
Rathke, 18
Ratitæ, 612
Rats, 639
Rat-tail larva, 493
Rattlesnake, 601
Ray, 10, 20
Réamur, 13
Receptaculum seminis, 120, 471
Rectrices, 604
Rectum, 461
Red coral, 256
Redia, 276
Reduviidæ, 489
Regulares, 345
Reindeer, 642
Remak, 18
Remiges, 604
Remora, 577
Renilla, 258, 259
Reproduction, asexual, 140, 143
Reproduction, sexual, 142
Reptilia, 588
Respiratory organs, 107
Respiratory organs of vertebrates, 547
Reticularia, 196
Reticulum, 642
Retina, 129, 131
Retina of vertebrates, 540
Retinaculum, 494
Retinula, 405
Retitelariæ, 453
Rhabdites, 270
Rhabditis, 300
Rhabdocœlida, 269, 271
Rhabdom, 129, 405
Rhabdonema, 145, 300
Rhabdopleura, 514
Rhachiglossa, 380
Rhachis, 414
Rhamphastos, 616
Rhea, 613
Rhegmatodes, 242
Rhinoceros, 641
Rhinocerotidæ, 641
Rhinoderma, 585
Rhizocephala, 426
Rhizocrinus, 342
Rhizopoda, 187
Rhizostomeæ, 250
Rhopalocephalus, 213
Rhopalocera, 495
Rhopalonema, 234
Rhynchobdellidæ, 321
Rhynchobothrium, 286
Rhynchocephalia, 596
Rhynchonella, 325, 328
Rhynchophora, 485
Rhynchota, 489
Rhytina, 645
Rib, 517, 518
Right whale, 646
Ring canal, 331
Rocky Mountain sheep, 643
Rodentia, 638
Rods and cones, 129, 540
Root barnacles, 426
Rorqual, 646
Rösel von Rosenhofen, 13
Rossia, 395
Rostellum, 280
Rostrum, 389, 424, 465
Rotalia, 188, 198
Rotatoria, 293
Rotifera, 293
Round worms, 298
Rove beetles, 484
Rudistidæ, 368
Rugosa, 258
Rumen, 641
Ruminantia, 641
Rupicapra, 642

Sabellidæ, 313
Sabinea, 435
Sable, 647
Sacconereis, 311
Sacculina, 426
Sacculus, 128, 542
Saccus vasculosus, 563
Sacral ribs, 528
Sagartia, 259
Sagitta, 296
Sagitta (ear bone), 564
Sagitta, development of, 158
St. Hilaire, 14, 22
Salamandra, 585, 587
Salamindrina, 587
Salinella, 220
Salivary glands, 106
Saltatoria, 480
Saltigrada, 453
Salmo, 576
Salmon, 576
Salmonidæ, 576
Salpa, 510, 512
Salpæformes, 510
Sand dollar, 345
Sand saucers, 380
San José scale insect, 490
Sapajous, 651
Sapphirina, 421
Sarcocystis, 213, 218
Sarcode, 60
Sarcolemma, 93
Sarcophaga, 493
Sarcophilus, 633
Sarcopsylla, 494
Sarcoptes, 454
Sarcosepta, 255
Sarcosporida, 218
Sarsia, 241
Saurii, 598
Sauropsida, 588
Sauruæ, 612
Savigny, 14
Savigny's law, 401
Sawfish, 572
Sawflies, 485, 486
Saxicava, 367
Saxicavidæ, 368
Scala media, 543
Scala tympani, 543
Scala vestibuli, 543
Scale insects, 490
Scale, placoid, 515
Scales of fishes, 515, 558
Scales of reptiles, 597
Scallops, 637
Scalpellum, 424
Scansores, 616
Scansorial foot, 614
Scape, 603
Scaphander, 381
Scapharca, 367
Scaphiopus, 588
Scaphognathite, 431
Scaphopoda, 369
Scapula, 528
Scarabæidæ, 484
Schäffer, 13
Schizodont hinge, 359
Schizopoda, 428
Schizopodal appendages, 409
Schizosomi, 437
Sclerophylla, 261
Schleiden-Schwann theory, 58
Schwann, sheath of, 96
Scincidæ, 599
Sciuridæ, 639
Sciuromorpha, 639
Sciuropterus, 639
Sciurus, 639
Sclera, 131, 539
Scleral bones, 611
Sceleporus, 599
Scelrophyllia, 257
Sclerosepta, 255
Sclerotic, 539
Sclerotic bones, 593
Sclerotic coat, 130, 131
Sclerotomes, 531
Scolex, 278
Scollops, 367
Scolopax, 615
Scolopendra, 460, 461
Scolopendrella, 497
Scolopendridæ, 461
Scomber, 577

Scombridæ, 577
Scops, 617
Scorpionida, 447
Sculpin, 577
Scutellum, 489
Scutibranchia, 378
Scutigera, 461
Scutigeridæ, 461
Scutum, 424
Scyphomedusæ, 245
Scyphopolyp, 230
Scyphostoma, 245, 246
Scyphozoa, 245
Sea anemones, 251, 259
Sea cucumbers, 346
Sea fans, 259
Sea horse, 578
Sea lion, 648
Sea pens, 259
Sea otter, 647
Sea snakes, 601
Sea squirts, 505, 508
Sea urchin, fertilization of, 149
Sea urchins, 343
Sea whips, 259
Seals, 648
Secodont teeth, 626
Secondaries, 604
Secondary bones, 515
Secreta, 73
Sedentaria, 313, 453
Segmental organs, 116, 308
Segmentation cavity, 155
Segmentation of egg, 149, 151
Segments of head, 536
Selachii, 570
Selection, artificial, 43
Selection, natural, 44
Selection, sexual, 46
Selenodont teeth, 626
Semæostomæ, 250
Semicircular canals, 128, 542
Semilunar valves, 567
Semipalmate foot, 614
Semiplumes, 604
Sensations, 125
Sense organs of vertebrates, 537
Senses, 125
Sensory epithelium, 73, 82
Sensory organs, 125
Sepia, 386, 388, 395
Septibranchiata, 368
Septum, 306
Sericteria, 494
Serosa, 473
Serpulidæ, 313
Serranidæ, 577
Serripes, 368
Sertularia, 242
Serum, blood, 88
Sesiidæ, 495
Seventeen-year locust, 489, 490
Sexual cells, 143
Sexual epithelium, 78
Sexual glands, 78, 80
Sexual organs, 80, 117
Sexual organs of vertebrates, 550
Sexual reproduction, 142, 145
Sexual selection, 49
Shad, 576
Shagreen, 569
Sharks, 571
Sheath of Schwann, 96
Sheep, 642
Sheep tick, 493
Shell gland, 411
Shell, layers of, 361
Ship worms, 368
Shore crab, 437
Shoulder blade, 528
Shoulder girdle, 527
Shrews, 637
Shrimp, mantis, 429
Shrimp, opossum, 428
Siala, 616
Sialidæ, 482
Sialis, 482
Sicyonia, 434
Siderone, 47
von Siebold, 18
Silenia, 368
Silicispongiæ, 226
Siliqua, 367
Silkworms, 495
Silurian, 180
Siluridæ, 576

Silverfish, 477
Simia, 651
Simiidæ, 651
Simuliidæ, 493
Sinupalliata, 368
Sinus frontalis. 539
Sinus, sphenoid, 539
Siphon, 345, 387, 360
Siphonaptera, 493
Siphonophora, 240, 243
Siphonophores, 166
Siphonostomate, 371
Siphonostomata, 422
Siphuncle, 388
Sipunculoida, 317
Sipunculus, 317
Siredon, 36
Siren, 586
Sirenia, 644
Sirex, 485
Siricidæ, 486
Sixth sense, 125, 538
Skalis, 571
Skin, 76
Skull, 519
Skull of mammals, 619
Skunk, 647
Skylark, 616
Slime animals, 198
Slime eels, 557
Slime moulds, 198
Sloths, 636
Smell, organs of, 126
Smelt, 576
Snakes, 600
Snapping turtle, 596
Snout beetles, 485
Snow flea, 477
Social animals, 167
Soft-shell crab, 437
Soft-shelled turtle, 596
Solasteridæ, 337
Sole, 578
Solemyidæ, 367
Solen, 368
Solenoconchæ, 369
Solenogastres, 358
Solenoglypha, 601
Solenoglyphic tooth, 600
Solenidæ, 368
Solidungula, 641
Solifugæ, 449
Solpuga, 450
Solpugida, 449
Somatic cells, 143
Somatic layer, 159
Somatopleure, 159
Somites, 305
Song birds, 616
Sorex, 637
Soricidæ, 637
Sowbug, 442
Spadella, 298
Spadix, 238
Spanish flies, 484
Span worms, 494
Spatangoidea, 346
Species, 10
Species, nature of, 19, 25
Species, physiological characters of, 27
Spelerpes, 587
Speotyto, 617
Spermaceti, 646
Spermatophore, 392
Spermatozoa, 81
Spermatozoids, 202
Sperm nucleus, 149
Sperm whale, 646
Sphæridia, 330
Sphærogastrida, 451
Sphæroma, 442
Sphæromidæ, 442
Sphærophrya, 212
Sphærozoidæ, 195
Sphargis, 595
Sphenethmoid bone, 581
Sphenodon, 596
Sphenoidalia, 521
Sphenoid bone, 523, 620
Sphenoid sinus, 539, 624
Sphenopalatine ganglion, 537
Sphenotic bone, 522
Spherical animals, 135
Sphingina, 495
Sphyranura, 274
Spicula, 300

Spicules of sponges, 225
Spider crab, 436, 437
Spider monkeys, 651
Spiders, 451, 452
Spinal canal, 517
Spinal ganglion, 533
Spindle, directive, 146
Spindle fibres, 69
Spindle, nuclear, 68
Spinnerets, 452
Spinous process, 517
Spiny ant eaters, 632
Spiny lobster, 436
Spiracle, 459, 524, 544
Spiral valve, 565
Spirifer, 328
Spirorbis, 313
Spirobolus, 497
Spirula, 388, 394
Spirulidæ, 394
Spittle bug, 489
Splanchnic layer, 159
Splanchnopleure, 159
Spleen, 550
Splenial bone, 582
Splint bones, 640
Spondylidæ, 367
Sponge, fresh-water, 133
Sponges, 221
Spongida, 221
Spongilla, 133, 221, 227
Spongillidæ, 227
Spongioplasm, 61
Spontaneous generation, 31
Sporangia, 199
Spores, 213, 215
Sporoblasts, 185, 213, 215
Sporocyst, 276
Sporosacs, 238
Sporozoa, 213
Sporozoites, 185, 213, 215
Springtails, 477
Sprinkling-pot shell, 368
Spumellaria, 195
Squali, 571
Squalus, 571
Squamata, 597, 636
Squamosal bone, 526
Squid, 395
Squilla, 429
Squirrels, 639
Staggers, 493
Stapes, 525
Staphylinidæ, 484
Starfish, 333
Statoblasts. 227, 323
Statoliths, 128
Stauromedusæ, 250
Steganopodes, 615
Stegocephali, 586
Stegosaurs, 597
Stellate ganglion, 390
Stelmatopoda, 323
Stemma, 403
Stenops, 649
Stenson's duct, 539
Stentor, 209
Stephalia, 244
Stephanocyphus, 250
Sterna, 615
Sternaspis, 314
Stercoral pocket, 445
Sternum, 462, 518
Sticklebacks, 577
Stigmata, 459
Sting, 472, 486
Sting rays, 572
Stipes, 463
Stink bug, 489
Stolo prolifer, 512
Stomach, 106
Stomatopoda, 429
Stomodæum, 104
Stomolophus, 251
Stone canal, 330
Stone flies, 479
Storks, 615
Stratified epithelium, 73, 74
Stratum corneum, 76, 514
Stratum Malpighi, 76, 514
Streaming of protoplasm, 62, 188
Strepsiptera, 483
Streptoneury, 373
Stridulating organs, 469
Striges, 617
Strix, 617

Strobila, 249, 278
Strongylidæ, 301
Strongyloides, 300
Strongylocentrotus, 345
Strongylosoma, 497
Struggle for existence, 44
Struthio, 613
Struthiones, 613
Sturgeon, 573
Sturgeon, tail of, 41
Stylaster, 241
Style, crystalline, 364
Stylochus, 271
Stylohyoid ligament, 621
Styloid process, 621
Stylommatophora, 383
Stylonychia, 211, 212
Stylopidæ, 483
Stylops, 483
Subcutaneous tissue, 514
Subintestinal ganglion, 374
Subintestinal vein, 548
Submentum, 464
Subneural gland, 509
Subumbrella, 234
Suckers, 576
Suck fish, 577
Suctoria, 212
Suidæ, 641
Sulci, 535
Summer eggs, 416
Sun animalcules, 190
Supporting cells, 83
Supporting layer, 230
Supraintestinal ganglion, 374
Supraoccipital bone, 522
Supraœsophageal ganglion, 123
Suprascapula, 528
Surf perch, 577
Sus, 641
Swallows, 616
Swallow tails, 496
Swammerdam, 13
Swans, 615
Swarm spores, 185, 195
Sweat glands, 618
Swell fish, 578
Swim bladder, 547
Swimming bell, 243
Swimming birds, 614
Swine, 641
Sword fish, 577
Sycandra, 222, 225
Sycon, 223, 225
Sycones, 225
Syllidæ, 313
Syllis, 311
Sylvicolidæ, 616
Sylvius, 12
Symbiosis, 169
Symmetry, 134
Sympathetic coloration, 46
Sympathetic system, 537
Symplectic bone, 561
Symphyla, 497
Synapta, 349
Synapticula, 257
Synascidiæ, 510
Syncitia, 71
Syncœlidium, 269, 271
Syncoryne, 241
Synentognathi, 575, 576
Syngamus, 301
Syngnathus, 578
Syringopora, 259
Syrinx, 608
Syrphidæ, 493
Systems of organs, 100
Systemic circulation, 549
Systemic heart, 391

Tabanidæ, 493
Tabulæ, 257
Tabulatæ, 257
Tactile bristles, 126
Tactile corpuscle, 537
Tactile organs, 125
Tadpole, 586
Tadpoles of Rana temporaria, 35
Tænia, 169, 279, 282
Tæniadæ, 287
Tæniolæ, 246
Tænioglossa, 380
Talpa, 637
Talpidæ, 637
Tanais, 442

Tanystoma, 492
Tapetum nigrum, 131, 540
Tape worms, 285
Tapiridæ, 641
Tapirs, 641
Tapirus, 641
Tarantula, 453
Tardigrada, 455, 636
Tarsal bones, 529
Tarsus, 463
Tarsiidæ, 649
Tarsius, 649
Tarso-metatarsus, 607
Tasmanian devil, 633
Taste, organs of, 126
Taste organs of vertebrates, 538
Tatusia, 636
Tautoga, 576
Taxidea, 647
Taxodont hinge, 359
Tectibranchia, 381
Tectrices, 604
Teeth, dermal, 515
Teeth of mammals, 624
Teeth of vertebrates, 547
Tejidæ, 599
Tejus, 599
Telea, 495
Teleostei, 574
Teleostomi, 569
Tellina, 368
Tellinidæ, 368
Telolecithal eggs, 152
Telson, 427
Telotroche, 309
Temporal bone, 620
Temperature of mammals, 630
Tendinous tissue, 85
Tenebrionidæ, 484
Tentacles, gastral, 246
Tentaculata, 264
Tent caterpillars, 495
Tenthredinidæ, 486
Terebella, 108, 313
Terebellidæ, 313
Terebra, 486
Terebrantia, 486
Terebratulina, 328
Teredo, 368
Teredidæ, 368
Tergum, 424
Termes, 478
Termitidæ, 478
Terns, 615
Terrapin, 596
Terricola, 315
Tertiary, 181
Tessellata, 342
Tesseridæ, 250
Testicardines, 328
Testudo, 596
Testudinata, 594
Testudinidæ, 596
Tethyoidea, 508
Tetrabothrium, 286
Tetrabranchia, 394
Tetracoralla, 258
Tetractinellidæ, 227
Tetramera, 484
Tetraonidæ, 614
Tetrapneumones, 453
Tetrapoda, 555
Tetrarhynchidæ, 286
Tetrarhynchus, 281, 286
Tetrastemma, 290, 291
Tetrasticta, 453
Tetraxonia, 226
Tettix, 481
Thalamophora, 196
Thalamus, 534
Thalassicola, 192
Thalassicolidæ, 195
Thalassima, 317
Thalassochelys, 596
Thaliacea, 510
Thamnocnida, 242
Thaumantia, 242
Theca, 255, 338
Thecasomata, 382
Thelepus, 313
Thelyphonida, 448
Thelyphonus, 448
Theridium, 453
Theriodonta, 594
Theromorpha, 594
Thoracici, 562

Thoracic fin, 526, 562
Thoracostraca, 427
Thread cells, 229
Thrips, 479
Thrushes, 616
Thylacinus, 633
Thymus gland, 547, 577
Thyone, 349
Thyroid gland, 547
Thysanoptera, 479
Thysanozoon, 271
Thysanura, 477
Tiara, 236
Tiaris, 242
Tibia, 463, 529
Tibiale, 529
Tibio-tarsus, 607
Ticks, 454
Tick, sheep, 493
Tiedemann's vesicles, 331
Tiger, 647
Tiger beetles, 484
Tillodontia, 643
Tima, 242
Tinea, 494
Tineidæ, 494
Tipulidæ, 492
Tissues, 71
Tissues, accessory, 99
Tissues, classification of, 72
Tissues, connective, 83
Tissues, elastic, 85
Tissues, epithelial, 73
Tissues, muscular, 91
Tissues, nervous, 94
Tissues, principal, 99
Tissues, tendinous, 85
Toad, horned, 599
Toads, 588
Tobacco worm, 495
Tocogony, 140
Tomato worm, 495
Tongue bone, 524
Toothed birds, 612
Tooth shells, 369
Tornaria, 513
Torpedinidæ, 572
Torpedo, 572
Tortoises, 594
Tortoise shell, 596
Tortricidæ, 494
Total cleavage, 152
Totipalmate foot, 614, 615
Toucans, 616
Toxiglossa, 380
Toxodontia, 643
Toxopneustes, 345
Trabeculæ, 520
Trachea, 109, 443, 458, 547
Tracheal gills, 469
Trachydermon, 357
Trachymedusæ, 239, 242
Trachynema, 242
Tractus olfactorius, 534
Tragulidæ, 642
Tragulus, 642
Transverse commissure, 123
Transverse process, 518
Trapdoor spider, 453
Tree cricket, 481
Tree hoppers, 490
Tree toads, 588
Trematoda, 271
Triarthus, 415
Triassic, 180
Triaxonia, 226
Trichechidæ, 648
Trichechus, 648
Trichina, 302
Trichocephalus, 302
Trichocysts, 205
Trichodectes, 479
Trichomonas, 202
Trichoplax, 220
Trichoptera, 483
Trichotrachelidæ, 302
Triclalidæ, 269, 271
Triconodont teeth, 626
Tridacna, 367
Trigeminal nerve, 536
Trilobitæ, 414
Trimera, 485
Trionychia, 596
Tristicta, 453
Tristoma, 274
Tritocerebrum, 462, 468

Triton, sections of embryo, 39
Tritonidæ, 382
Tritubercular teeth, 626
Tritylodon, 632
Trivium, 334
Trochal disc, 293
Trochanter, 463
Trochidæ, 379
Trochilidæ, 616
Trochilus, 616
Trochlear nerve, 536
Trochophore, 306
Trochosa, 453
Trochus, 379
Troctes, 479
Troglodytidæ, 616
Troglodytes, 651
Trombididæ, 454
Trophi, 294
Tropic birds, 615
Tropidonotus, 601
Trout, 576
Trunk fish, 578
Trutta, tail of, 41
Trygonidæ, 572
Tubicola, 313
Tubificidæ, 315
Tubinares, 615
Tubifex, 315
Tubiporidæ, 259
Tubitelariæ, 453
Tubular glands, 77
Tubular nervous system, 124
Tubulariæ, 239, 241, 242
Tubulipora, 324
Tunic, 505
Tunicata, 505
Turbellaria, 268
Turbinated bone, 620
Turbinidæ, 379
Turbo, 379
Turbot, 578
Turbidæ, 616
Turdus, 616
Turkey, 614
Turkey buzzard, 617
Turritopsis, 240, 242
Turtles, 594
Twixt brain, 534
Tylenchus, 300
Tylopoda, 643
Tympanal organ, 128, 468
Tympanic annulus, 544
Tympanic bone, 526
Tympanic cavity, 621
Tympanic membrane, 544
Tympanum, 544
Type theory, 15
Typhline, 599
Typhlops, 601
Tyrian purple, 380
Tyrannidæ, 616

Uca, 437
Uintatherium, 643
Ulmaris, 247
Ulna, 529
Ulnare, 529
Umbilicus, 370, 554
Umbo, 358
Umbrella, 234
Uncinate process, 605
Ungues, 618
Ungulæ, 618
Ungulata, 639
Unguligrade, 640
Unicellular glands, 77
Unicorn, 646
Unio, 367
Unionidæ, 367
Ureter, 550
Urinary bladder, 552
Urinator, 615
Urinatores, 615
Urnatella, 322
Uroceridæ, 486
Urochorda, 505
Urodela, 587
Urogenital sinus, 553
Urogenital system, 120
Urogenital system of vertebrates, 550
Urosalpinx, 379, 380
Ursidæ, 647
Ursus, 647
Use and Disuse, 55, 99
Uterus, 120, 629

Utriculo-saccular duct, 542
Utriculus, 128, 542

Varanus, 599
Vacuole, contractile, 183
Vacuole, food, 183
Vagabundæ, 453
Vagina, 120, 629
Vagus nerve, 536
Valkeria, 324
Vampyre, 638
Vanessa, 496
Varanidæ, 599
Variation, 25
Vas deferens, 120
Vasa Malpighii, 461
Vascular arches, 504
Vater Pacinian corpuscles, 126
Vegetative organs, 101
Vegetative pole, 147, 151
Veins, 112
Velella, 245
Veliger, 355, 364
Velum, 235, 356
Veneridæ, 368
Ventral aorta, 548
Ventral fin, 562
Ventral nerve cord, 123
Ventricles of brain, 534
Ventricle of heart, 111, 548
Venous sinus, 567
Venus, 368
Venus' flower basket, 226
Venus' girdle, 264
Vermiform appendix, 627
Vermilinguia, 599, 636
Vermes, 535
Vertebra, 518
Vertebra (of ophiuroids), 337
Vertebral column, 516
Vertebrata, 514
Vertex, 462
Vesal, 12
Vesicle, auditory, 127
Vesicle, blastodermic, 155
Vesicle, germinal, 146
Vesicle, Polian, 331
Vesicle, Tiedemann's, 331
Vesicularia, 324
Vesicula seminalis, 120
Vesparıæ, 487
Vesperlilionidæ, 638
Vesperugo, 638
Vibracularia, 323
Vibrissæ, 618
Viperidæ, 601
Visceral ganglia, 353
Visceral sac, 351
Visceral skeleton, 523
Vitellarium, 267
Vitreous body, 130
Vitrodentine, 558
Viviparous, 161
Vogt, 24
Volutidæ, 380
Volvocina, 202
Volvox, 202
Vomer, 525
Vortex, anatomy of, 120
Vorticella, 211
Vorticellidæ, 210

Wading birds, 615
Wagner, 24
Waldheimia, 326
Walking stick, 480
Wallace, 24
Wallace's line, 177
Walrus, 648
Warblers, 616
Warm-blooded animals, 114
Wasps, 487
Water bears, 455
Water beetles, 484
Water scorpion, 489
Water snake, 601
Water-vascular system, 115, 330
Weasel, 647
Weevils, 485
Weismann, 24
Whalebone, 645
Whales, 645
Whelks, 380
White ants, 478
White fish, 576
White matter, 124, 532

UNIVERSITY OF CALIFORNIA MEDICAL SCHOOL LIBRARY

THIS BOOK IS DUE ON THE LAST DATE
STAMPED BELOW

Nov 1. 1919
NOV 18 1919
DEC 6 1919
FEB 10 1920
Oct. 19
Nov. 1
Nov. 15
MAY 4 - 1929
[illegible]
MAR 1 - 1937
NOV 1 - 1941

1m-11,'18

QL48 H57k 1905	Hertwig, R. A manual of zoology.	5720
R. Millzner	1/24/23 FEB 7 1923	FEB
Rubin	MAY 1 - 1929	MAY 3 - 1929
W. L. Terry	APR 30 1934	
Renewed	MAY 15 1934	SEP 5 1934
		FEB 25 1937
M. Kleberz	MAR 1 - 1937	
J. Buff	NOV 1 - 1941	DEC 23 1941

5720

University of California Medical School Library

UNIVERSITY OF CALIFORNIA MEDICAL SCHOOL LIBRARY

THIS BOOK IS DUE ON THE LAST DATE
STAMPED BELOW

Nov 1. 1919
NOV 1 8 1919
DEC 5 1919
FEB 1 0 1920
Oct. 19
Nov. 1
Nov. 15
MAY 4 - 1929
[illegible]
MAR 1 - 1937
NOV 1 - 1941

1m-11,'18

QL48 Hertwig, R.
H57k A manual of zoology.
1905 5720

R. Millzner	FEB 7 1923 1/24/23	FEB
Rubin	MAY 1 - 1929	MAY 3 - 1929
W. L. Terry	APR 30 1934	
Renewed	MAY 15 1934	~~SEP 5 1934~~
M. Klentz	MAR 1 - 1937	FEB 25 1937
J. Buff	NOV 1 - 1941	DEC 23 1941

5720

University of California Medical School Library